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STOCK CONCEPT INTERNATIONAL SYMPOSIUM

October, 1980

Sponsored by

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Ann Arbor, Michigan, USA

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Foreword to the Stock Concept Symposium

Man's development of the Laurentian Great Lakes Basin has placed major, continuing, cumulative stresses on the Great Lakes ecosystem and its fish populations. What had been a relatively simple, slowly evolving, stable fish fauna reacted with spawning failures, extreme fluctuations between population crashes and remarkable recoveries, intense interspecific competition, extinction of some species, and losses of many discrete stocks.

Governments responded with a series of efforts between 1893 and 1952 to establish international fishery commissions or cooperative regulatory and management programs to bring order to the troubled commercial fishery shared by the eight states and one province whose jurisdictions extend into the lakes (Fig. 1). The efforts failed until the sea lamprey (*Petromyzon marinus*), a parasitic predator native to the Atlantic Ocean, became established in the upper three lakes. Its effect on fish populations was recognized as an impending international catastrophe. Given this added threat to the fishery, governments recast earlier efforts, and quickly drafted and ratified the 1955 Convention on Great Lakes Fisheries. The convention established the Great Lakes Fishery Commission (GLFC) to develop and coordinate fishery research programs, to advise governments on measures to improve the fisheries, and to develop measures and implement programs to control sea lamprey.

The commission's programs, undertaken with its principal cooperators, the Great Lakes states, the Province of Ontario, and the U.S. and Canadian federal governments, gradually brought sea lamprey to levels that allowed for survival and growth of desirable fish species, first in Lake Superior, and then in Lakes Michigan, Huron, and Ontario. Fishery scientists, envisioning the tremendous potential for fishery development, enthusiastically turned their attention to rehabilitation of Great Lakes fishery resources. However, there were more questions than answers, and the commission felt a great responsibility to ensure continuing development of knowledge, synthesis of what was already known, and its application to Great Lakes fishery management.

As one way to meet this responsibility, the commission has promoted a series of symposia by active participation and varying degrees of financial and developmental support. These symposia include, in 1971, the international symposium on Salmonid Communities in Oligotrophic Lakes (SCOL) (J. Fish. Res. Board Can., Vol. 29, No. 6); 1972, Bio-Engineering Symposium for Fish Culture; 1976, the Percid International Symposium (PERCIS) (J. Fish. Res. Board Can., Vol. 34, No. 10); 1978, A Symposium on Selected Coolwater Fishes of North America (Kendall 1978); 1979, the Sea Lamprey International Symposium (SLIS) (Can. J. Fish. Aquat. Sci., Vol. 37, No. 11); 1979; Bio-Engineering Symposium for Fish Culture (Allen and Kinney 1981); and now the Stock Concept Symposium (STOCS) (Can. J. Fish. Aquat. Sci., Vol. 38, No. 12).

The STOCS had its formal beginnings at the GLFC 1976

FIG. 1. Fishery jurisdiction in the Great Lakes. The boundary between Ontario and various states is also the international boundary between Canada and the United States. The natural and man-made waterways between the lower lakes and the Atlantic Ocean are also shown (Fetterolf 1980).

Annual Meeting when the Lake Ontario Committee, concerned that current stocking practices would lead to genetic dilution and impairment of established self-reproducing stocks, recommended in part that a policy statement based on the "stock concept" be developed by the commission and that its Scientific Advisory Committee (SAC) be instructed to examine the problem, specify guidelines and references, and recommend appropriate research.

In responding for the commission, Chairman K. H. Loftus noted that similar recommendations had been submitted by the Upper Great Lakes Committees. He stated that the commission is in full accord with the expressed concern, and said that the commission was considering initiation of a large-scale international symposium to address the whole question of the stock concept and needs for research in fish genetics and selection, as applied to rehabilitation of Great Lakes fish stocks. The commission charged its SAC to investigate the feasibility of such an undertaking.

The remainder of this story is told by the STOCS Steering Committee Co-chairmen in their introduction to these proceedings (Berst and Simon 1981).

For those readers who wish to know more about the commission, its history and operations, see Fetterolf (1980); about the history of sea lamprey in the Great Lakes see Smith and Tibbles (1980) and Pearce et al. 1980; or about the history of man's effects on the Great Lakes and their fish populations, see Berst and Spangler 1973; Christie 1973; Hartman 1973; Lawrie and Rahrer 1973; Smith 1972; and Wells and McLain 1973.

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Introduction to the Proceedings of the 1980 Stock Concept International Symposium (STOCS)[1]

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The Stock Concept International Symposium (STOCS) was one of a series of symposia supported and/or sponsored by the Great Lakes Fishery Commission. STOCS was held at the Nottawasaga Inn, Alliston, Ontario, September 29 to October 9, 1980. The symposium was a major initiative to synthesize knowledge on the stock concept in its present and potential applications to fish populations. Clarification was sought on needs for research, especially as applied to the rehabilitation of Great Lakes fish stocks.

The rationale for the symposium evolved as a result of the increased interest and level of perception by the scientific community in the structure of fish populations and the acceptance of the concept that fish species are subdivided into more or less distinct or discrete subpopulations or stocks. It is also becoming widely accepted that the stresses of cultural eutrophication, exploitation, and species introductions are effective on fish communities at the stock level. Adaptive as well as nonadaptive changes occur in wild and hatchery (domesticated) stocks. Irreversible losses of genetic material may occur, with serious consequences for the fisheries that depend on healthy populations. Because of these pressures, it was essential to gain an understanding of the way in which various stresses can affect genetic resources.

STOCS was planned as a workshop-type conference by a Steering Committee consisting of nine scientists representing the Province of Ontario, and state and federal agencies in the United States. The Committee developed a comprehensive list of stock-related questions and problems in the Great Lakes and organized them into five tentative objectives for the symposium.

1) Develop a refined up-to-date stock concept based on sound ecological and genetic principles.

2) Examine the prospects and strategies for the preservation of gene pools.

3) Examine the potential for use of the stock concept in improving fish culture.

4) Seek applications of the stock concept in rehabilitation of freshwater fish resources.

5) Develop use of the stock concept in regulating fisheries.

At the outset, the Steering Committee recognized that these objectives might be considerably restructured as a result of deliberations during the synthesis sessions that concluded the conference.

For this symposium the Steering Committee and the Session Chairmen chose and invited a total of 86 fisheries experts from Europe, the west and east coasts of North America, and from the Great Lakes region to pool, synthesize, consolidate, and publish existing knowledge on fish stocks in an attempt to answer many of our questions. No attempt was made, through choice of participants, to cover exhaustively a single specialty, approach, or species. Hence, many excellent specialists were excluded from participation. Subject matter of the symposium was diversified deliberately to permit accom-

[1]This paper forms part of the Proceedings of the Stock Concept International Symposium (STOCS) convened at Alliston, Ontario, September 29–October 9, 1980.

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modation of different areas of specialization and to stimulate different points of view.

This diversity was deemed to be necessary because 1) monomorphic solutions to a broad spectrum of problems did not seem to be plausible; 2) several authorities enjoy, or regulate, the resources of the lakes — not all of these groups agree on fundamental issues such as apportionment or management of resources; 3) studies of Great Lakes species have been extensive, but not exhaustive — thus, we have reached out to other continents for guiding examples; 4) we did not envisage the assembly of a "mutual admiration society" to be maximally productive in drawing together the inferences of the participants as a consequence of their experiences at the symposium or in the surfacing of truly fresh ideas in the synthesis sessions which were intended to be the most labor-intensive segment of the conference.

Despite these elements of planned diversity, there was commonality of purpose at the conference in interest and concern about stocks. We hope that the readers of these proceedings will find that this theme of commonality provides a basis for the assimilation of new attitudes and ideas that will be useful in current programs and those of the future.

We do not believe it is possible to provide everything for everyone. We do believe that some building materials, among the variety assembled, will find use for the enlargement of a good many viewpoints.

A general outline of the program of the STOCS conference follows:

- Introductory Session
- Keynote Perspectives
- Background Papers
- Historical and Current Evidence of the Stock Concept and its Applications
  - European Waters
  - North American Coastal Waters
  - North American Inland Lakes
  - Great Lakes
- Synthesis Sessions

Acknowledgments

It is a pleasure to acknowledge our appreciation to the numerous collaborators who gave generously of their time and energies in the planning and implementation of the symposium, the preparation of manuscripts, and publication of the proceedings. We are especially indebted to other members of the Steering Committee: J. M. Byrne, W. J. Christie, P. E. Ihssen of Canada; H. E. Booke, E. H. Brown Jr., R. L. Eshenroder, and R. J. Poff of the United States. The committee developed the program and invited the participants. The synthesis sessions of the symposium were planned and coordinated by J. F. Koonce and G. R. Spangler. General sessions were convened by H. E. Booke, J. M. Byrne, J. M. Fraser, R. M. Horrall, P. E. Ihssen, P. A. Larkin, R. J. Poff, R. L. Saunders, J. E. Thorpe, and D. A. Webster.

Others sharing in the planning of STOCS were A. H. Lawrie, K. H. Loftus, and H. A. Regier. Margaret Ross of the GLFC Secretariat served as secretary for the Steering Committee and provided liaison between the committee and the Commission.

We thank C. M. Fetterolf Jr., A. Lamsa, and B. Biedenbinder of the GLFC Secretariat for their advice and for many thoughtful courtesies to the Steering Committee.

The secretarial duties so ably performed by Ruth Koerber, Margaret Hamilton, Betty McEachern, and Rita Mitchell, and the arrangements by Fred Dahl, were greatly appreciated by everyone at the conference. Special thanks are due to Allan Wainio, who handled the difficult task of local transportation of the delegates at the symposium. Al's good humor and enthusiasm were much appreciated by all of the delegates.

Financial support for the symposium was provided by the Great Lakes Fishery Commission.

Finally, with special gratitude, we acknowledge the patience and editorial abilities of Win Billingsley and David Cook, who made the publication of these proceedings possible.

Who's In Charge Here?[1]

JACK R. HARLAN

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It is as if man had been suddenly appointed managing director of the biggest business of all, the business of evolution . . . whether he is conscious of what he is doing or not, he is in point of fact determining the future direction of evolution on this earth. That is his inescapable destiny, and the sooner he realizes it and starts believing in it, the better for all concerned.

Julian S. Huxley 1957

HUXLEY wrote *New Bottles for New Wine* nearly a quarter century ago; his message has been slow to sink in. One reason, perhaps, is that we often upset natural balances with the innocence of ignorance. There is nothing criminal or evil in growing potatoes in Colorado. The Colorado potato beetle (*Leptinotarsa decemlineata*) had been feeding on buffalo bur (*Solanum rostratum*) and other native species of *Solanum*, and its known distribution was confined to the east slope of the Rocky Mountains. Potato is also a *Solanum*, and as settlers began to grow it in Colorado, the beetle transferred its feeding grounds. It prospered, spread all over North America, and found its way to Europe and other potato-growing regions. As it became more a beetle of the world, it found tobacco, peppers, and eggplant to its liking. We have raised this obscure insect from rural Colorado to the position of world traveler and pest of distinction (Atkins 1978).

One must wonder about the alfalfa butterfly, *Colias eurytheme*. It is a native Californian that used to feed on scattered wild legumes and was once a rare species. Now that we grow alfalfa on a large scale, the butterfly has become common and in some areas often attains pest status.

Again, in the spirit of development and improvement, we managed to plant a carpet of wheat from northern Mexico well into Canada. The wheat belt is interrupted here and there with patches of barley, oats, and rye and with sorghum, cotton, alfalfa, and the like, but the interruptions do not interfere with the yearly migrations of rust diseases. Infections begin along the Rio Grande each year and spores are blown northward; the spores alight on congenial hosts, germinate, infect, feed, and multiply. The mass of spores increases with each cycle and the rusts move northward, feeding on stems or leaves as they go (Vanderplank 1975).

In the northern end of the wheat belt the rusts cannot overwinter, so that new infection must arrive each year if the wheat is to become rusted. Also, the rusts cannot oversummer in the southern part of the belt, so spores must be blown southward to infect winter wheat and renew the spring migration. We have created a gigantic epidemiological system in which several species of *Puccinia* migrate yearly over 4000 km. The system must be included among the marvels of the biological world.

Needless to say, the system has caused enormous economic loss from time to time. The variety Marquis, bred in Canada, was introduced into the northern plains in 1912 and soon became the dominant wheat, partly because of its rust resistance. The rust epidemic of 1916 took it out. Farmers turned to durum wheats. Race 11 of rust caused severe damage in them. Ceres, a derivative of Marquis, gave an excellent performance from 1926 to 1934, when race 56 became the dominant race of rust. Severe epidemics in 1935 and 1937 took out Ceres. The epidemic of 1935 is estimated to have cost 160 million bushels in the U.S. alone (USDA 1965). Thatcher was resistant to race 56 and it, together with Hope and hybrid derivatives of both, managed to contain rust outbreaks for a few years. Then race 15B and an array of biotypes of it swept over North America in 1953 and 1954. McNew wrote in 1960: "In looking back over the past 50 years, one is impressed that the germ plasms of *Puccinia* and *Triticum* have been playing tag with each other. As soon as a new set of genes for resistance was introduced into the crop, the parasite developed a new race for virulence. In only 20 of the fifty years between the great epidemics of 1904 and 1954 was wheat adequately protected from *Puccinia graminis* on the Great Plains of North America."

The wheat belt is completely artificial, and I cannot find anything like it in nature. There are some species of native grasses that cover the same geographic range. Blue grama (*Bouteloua gracilis*) ranges from northern Mexico well into Canada and builds massive, nearly pure, stands over vast reaches of the High Plains. Western wheatgrass (*Agropyron smithii*) and little bluestem (*Andropogon scoparius*) occur over much of the same north–south range, but in more discontinuous stands. All three species are infected by rusts: blue grama by *Puccinia bartholomaei*, little bluestem by *P. andropogonis*, and western wheatgrass, being related to wheat, can be infected by *P. graminis* and *P. rubigo-vera*. No doubt spores of these rusts are also blown back and forth over the plains; but epidemics do not occur. One can find a few pustules on almost any plant, and they may be common on senescent leaves. Occasionally and locally when conditions are especially favorable for rust development, some minor damage may occur, but I have never seen a plant killed by rust. This is the natural balance one expects between host and parasite after a long period of coevolution.

It would be instructive to study the genetic defenses deployed by these grasses against the kind of diseases that have caused so much damage to our small grains crops. To date, plant pathologists have not studied the material in detail, perhaps because there has been no serious problem. Several grass breeders have looked into the genetic variability of the host species and we have found them to be extraordinally complex (Harlan 1958). In one study of blue grama over a restricted part of its range, we found chromosome races of $2n = 20$, 40, 60, 42, and 84, a series based on

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$x = 10$ and another on $x = 7$ in the same species (Snyder and Harlan 1953). Many thousands of single plant isolates have been grown in grass-breeding nurseries at several stations over many years. The genetic diversity displayed is simply on a different order from that deployed by the wheat crop over the same geographic range (Harlan 1976).

Several scientists with a similar frame of reference have been looking into genetic diversity and genetic defenses of populations of wild wheat, barley, and oats in Israel. Israel is a small country, but Nevo et al. (1979) and Brown et al. (1978) were able to demonstrate more electrophoretic diversity in wild barley in Israel than in a composite cross involving over 6000 cultivars from all over the world. Browning (1974) and Browning et al. (1977) were able to analyze genetic defenses of wild oat populations where individual races of crown rust could be identified. The defences deployed were found to be remarkably complex. General resistance, specific resistance (gene-for-gene), dilatory resistance (slow-rusting), tolerance, and perhaps other strategies all operated simultaneously. They found that if 30% of the plants of a population were resistant to even the most virulent race of crown rust, the whole population would be protected. Slow rusting can be critical in delaying the onslaught of an epidemic until it is too late to do much damage or until weather conditions are unfavorable for the parasite. There is much to be learned from natural ecosystems that would help us manage our agroecosystems.

The simplicity of our agroecosystems puts us at a great disadvantage. Nature is not so reserved. Traditionally, the most serious disease of oats in the midwest is crown rust. It was something of a victory when the Victoria cultivar was introduced from Uruguay with good resistance to the disease. The resistance was soon incorporated into several cultivars, all of which promptly collapsed before a disease so insignificant that it had not even been identified and the causal organism was unnamed. The new disease of oats was called victoria blight and the organism which had heretofore eked out an existence on native grasses received the epithet *Helminthosporium* (*Cochliobolus*) *victoriae*. How could one have predicted that resistance to one disease would cause extreme susceptibility to a disease that had not even been identified?

Some of our problems are caused by practices in which our innocence is something less than pristine. In response to periodic economic urges, we have, from time to time, cleared forests in the southeast and established farms that were abandoned before long. On the coastal plain especially, the loblolly pine (*Pinus taeda*) is the first tree to become established in old-field succession. It grows quickly and it seemed only reasonable to grow plantations of it rather than attempt to harvest random natural stands. To get seeds, most of the forest agencies, whether public or private, advertised that they would buy seed (good quality, of course) by the bushel. It was assumed that seeds purchased in this way would represent random sources and a genetic sampling roughly equivalent to natural diversity. One might have predicted that seeds obtained by this procedure would come mostly from runty, dwarfed, easy-to-climb trees — and they did. Untold hectares were planted to genetic runts that would assure low production (Dorman 1976).

Meanwhile, fusiform rust (*Cronartium fusiforme*) had made its mark in the form of cankers on both loblolly and slash pines. Its spread and distribution is documented by Dinus (1974), and its relationship to oak-alternate hosts discussed by Squillace et al. (1978).

Diseases of other southern pines have become more serious with plantation management as well: *Phytophthora cinamomi*, causing little-leaf disease and *Scirrhia acicola* causing brownspot needle blight on longleaf pine, are examples. As Bingham et al. (1971) pointed out, most of forest pathology is devoted to salvaging what man has brought about. The situation is rather general. Kozlowski (1980) recently stated: "Much of the forested land of North America is maintained in populations of single species, and great effort has been exerted to counteract normal plant succession and maintain these stands in temporary stages of development. More than half the sawtimber in the United States is comprised of a few subclimax species, including Douglas-fir (*Pseudotsuga menziesii*) and several southern pines such as loblolly pine (*Pinus taeda*), longleaf pine (*Pinus palustris*), slash pine (*Pinus elliottii*), and shortleaf pine (*Pinus echinata*)."

As recently as 20 years ago, no genetically improved seed of southern pines was available. By 1973, 11 southern states were using large volumes of certified seed, and some tree plantations are now yielding two to three times as much as plantations from average sources (Dorman 1976). But this could be an excellent device for finding obscure diseases and making them into household words. Blakeslee and Oak (1979) report on an outbreak of pitch canker (*Fusarium moniliforme*) on slash pine in Florida. In one 23-yr-old plantation, 24% of the trees were dead, 4% more expected to die within a year, and 94% of the remaining trees were infected. Under natural conditions the disease was so minor that it was not described until 1946 (Hepting and Roth 1946). One is repeatedly reminded of a statement by Vanderplank (1968): "Plant breeders and pathologists are busy patching their mistakes and bragging about how big the patches are."

Forest tree management must be something like fish rearing, in a genetic sense. It is impossible to raise a completely natural population under artificial conditions. We have it in our power to cut down every tree on earth, but we cannot replace a natural forest. If we must raise trees, we are forced to sample the genetic variability of natural populations. Our samples are necessarily restricted and cannot duplicate the genetic variability of the species. The same problem must face the hatchery man raising fish. I see no way that the natural diversity could be reproduced under artificial conditions. We can probably do better than we have done, but the replacement of natural populations by restricted samples leaves us vulnerable to pests, diseases, climatic stress, and other hazards.

Even small adjustments can cause problems. In central Texas, native pecan trees are sufficiently cold-tender that buds and small twigs are frozen, perhaps 2 years in five, and the crop is ruined. For commercial orchards it seems logical to select hardier stocks from farther north and avoid the occasional failures due to frost. However, freezing is a natural defence against insects; if buds are not frozen from time to time, insects build up to the point that crops are ruined every year instead of three to four times a decade (M. Harris, per-

sonal communication). The recent trend toward very large cattle feed-lot operations has resulted in serious and very expensive outbreaks of psoroptic cattle scabies (National Research Council 1979).

Most of our troubles we bring on ourselves, but few cases are so obvious as that of the gypsy moth (*Porthetria dispar*). It was imported from Europe in 1869 by a Leopold Trouvelot of Medford, Massachusetts, who hoped to cross it with the silkworm moth and develop a new textile industry (Graham 1972; Atkins 1978). The moth escaped and became a pest especially in or near urban developments. Masses of larvae could defoliate whole groves of trees. The infestation spread slowly and eventually became rather stable and quiescent in the 1930s and 1940s. Occasional local eruptions were a nuisance, however, and after World War II when DDT became available, campaigns were launched to eradicate the moth. By 1972, 100 million dollars had been spent and the situation was worse, not better. The moth spread farther and faster under spray than it did without spray. It is a hard lesson to learn. When DDT was outlawed, the USDA simply switched to Sevin and went on spraying (Graham 1972). More integrated systems have since been attempted, including the introduction of predators (Leonard 1974).

This relatively simple case was repeated severalfold in the cotton crop. There are a number of serious insect pests of cotton. Before effective general insecticides, the cotton industry was forced into earlier, shorter-staple cottons and some sanitation measures, as well as use of some degree of genetic resistance. A nearly reasonable accommodation between man, plant, and bug was evolving, but DDT changed all that. Sprays were effective, at first. As the pests became more resistant, rates of application and frequency of spraying increased. Insect populations began to change. Tobacco budworm (*Heliothis virescens*) erupted dramatically in the southeast because it became tolerant of the spraying regimes that killed off its predators. In California, where the boll weevil was absent, lygus bugs (*Lygus hesperus*) and pink bollworm (*Pectinophora gossypiella*) were the main pests, but soon insects that caused very minor damage before DDT became major threats to cotton, e.g. cabbage loopers, beet armyworms, etc. (Bottrell and Adkisson 1977). The situation passed from crisis to disaster. Shifting from DDT to organophosphates solved nothing; a whole new frame of mind had to be generated. More accurately, we returned to some of the old approaches worked out before DDT. The DDT mentality has to go, but it is hard for some people to grow out of it.

Proposals are still being made to spend vast sums to spray the imported fire ants, when these insects have been spreading under insecticide treatments for years (Lofgren et al. 1975). Spraying poisons is a simple thing to do but the ecological consequences can be complex. The destruction of natural enemies of the target species can easily make matters worse rather than better. The ramifications are often entirely unforeseen. Garcia and Huffaker (1979) report that efforts at malaria control in Bolivia resulted in killing household cats with a consequent increase in rodents and outbreaks of hemorrhagic fever.

Importations are often hazardous. The starling was deliberately imported to North America because some people thought it an attractive bird. It was released in central Park, New York City, in 1891 and reached the Pacific coast by 1950. It has probably filled a niche unwanted by most native birds, but it has preempted nesting sites and caused dramatic decline in some species. The eastern bluebird has probably suffered most. The introduction of African honey bees to Brazil has probably turned out better than we deserved. They are vicious and nervous bees, but they are better adapted to the tropics, and after crossing with European strains for a time, new races appear to be emerging that can be handled and that produce more honey. Brazilian bee keepers prefer the new strains to the less-adapted European bees (Michener 1975).

Among the most destructive importations are species that came unintentionally but were transported by man. Dutch elm disease has denuded thousands of towns and cities of their best shade trees. Chestnut blight has all but caused extinction of one of the finest forest trees of North America. White pine blister rust has caused enormous destruction in coniferous forests, and the imported fire ant has caused untold misery to man and his livestock. We could fill books with human blunders in trying to run the business of evolution, but perhaps this sample of horrors is enough to make the point. Let us turn to a few examples where we seem to have taken a few steps in the right direction or at least where things have turned out better than we were afraid they might.

The European rabbit was introduced to Australia in 1859 for sporting purposes. They bred like rabbits and progressed from nuisance to disaster. An especially virulent strain of myxoma virus was extracted from a South American rabbit and used to infect Australian rabbits. The epidemic that followed is one of the best known and most studied in history. We know the exact source of the infection and the time and place of release. Rabbits died by the millions. Within a few years, attenuated races of the myxoma had appeared and the occasional survivor becomes immune. Attenuated races have a selective advantage over the most virulent ones and are spread more readily by mosquito vectors (Fenner and Marshall 1957; Marshall and Fenner 1958). Gradually, rabbits and virus came to accommodate each other. Rabbit populations are nothing like they were before the myxoma epidemic, but there are still a lot of rabbits. It is surprising that a single constraint would prove so effective a control. A simple two-dimensional system is likely to be unstable, and additional factors may need to be introduced some time in the future.

The Australian rabbit control program became a model for other attempts. Some have succeeded and some have not. St. John's wort (*Hypericum perforatum*) was a serious weed pest introduced into California. It was brought under satisfactory control by the insect *Chrysolina quadrigemia* despite the fact that the insect was subject to predation by birds, mice, spiders, and earwigs. Attempts to control the same weed in Australia have failed because of predation (Goeden and Louda 1976). Puncture vine (*Tribulus terrestris*) has been brought under control in the U.S. southwest by two species of *Microlarinus* introduced from Italy. Australians had success in reducing cactus (*Opuntia*) infestation with the cactus moth, *Cactoblastis cactorum*, and this, despite more than 20 species of hymenopterous parasites that attack it. *Lantana camara* populations have been brought under control in Hawaii and

Fiji by *Teleonemia scrupulosa*, but the system backfired in Uganda where the insect transferred to cultivated sesame. Wapshere (1975) lists a number of successes with biological control procedures. Sometimes they fail because of predation or environmental conditions. The case of sesame in Uganda is the only one where the controlling insect became a pest and there was some indication that this would happen before the insect was introduced.

We seem to be making some progress in managing cotton insect pests (Bottrell and Adkisson 1977). Continuous spraying clearly led to a disaster. Now we are once again looking toward early cottons that can escape the peak populations that build up on long-season cottons. We are looking for more varieties with resistance or tolerance. We are paying more attention to sanitation, and we are looking at careful and precise use of insecticides to reduce the overwintering populations. The multiple approaches are already bringing good results in some areas.

In the puccinia path we have become more sophisticated in deployment of resistance genes (Knott 1972). By planting particular varieties in the south we can produce a screen such that only certain specified races of rust can pass enroute to the north. If the northern varieties are highly resistant to those races, rust can be kept to noneconomic levels. Most schemes of this sort divide the wheat belt into three zones with different arrays of genetic defense in each (Frey et al. 1977). Meanwhile, multilines seem to be working well in oats. Several have been released in Iowa and grown for several years on over $\frac{1}{2}$ million hectares without substantial loss due to crown rust, historically the most important disease of oats. Multilines are mixtures of lines that are essentially alike except that each line has a different set of alleles controlling reaction to disease.

In trying to manage our biological world, we are constantly pressed by genetic problems. What varieties should we deploy in field agriculture, what genetic stocks in our forests, or what stocks of fish should we rear? Even the introduction of biological control agents has genetic problems (Mackauer 1976). We have problems of source, population structure, genetic variability, selection, genetic drift, founder colony size, fluctuation in population size, changes due to artificial rearing. We are not capable of handling the genetic diversity of natural species; we must deal with samples. We cannot devise ecosystems as complex and stable as those in nature; we must deal with much simpler and much less stable systems.

Some problems appear to be solvable and we have had a few successes; others have defeated us. We have had great success with smallpox and may in fact have eliminated the disease completely. We have not fared so well with malaria. There was great confidence and enthusiasm in the early days of DDT and some regions were freed of the disease. But, as resistance built up, the incidence of malaria began to increase again. Although DDT has been outlawed in most of the world, some tropical countries are still using it in the vain hope of controlling the insect vectors. The usual method is to spray inside walls of houses to reduce the insult to the environment, but the technique is becoming less effective in Asia and never did work well in Africa. Malaria has returned to some regions that had been freed of it. The World Health Organizaiton tends to blame inadequate finances and poor support (Jeffery 1976), but Garcia and Huffaker (1979) suggest ". . . the basic problems undoubtedly are those that characterize any lost cause — underestimation of the enemy and overconfidence in the available weaponry."

We are woefully unprepared for the work we are about. We haven't much choice; we have to go ahead and blunder on. But we need to learn a great deal in a short time. We need to study natural ecosystems to see how they work — if we can find any left. We need to examine how species coevolve. We will be forcing coevolution and we would like it to come out right from our point of view. We need to be amazed and astonished and to recapture some of the awe and mystery of older societies. I consider Lewis Thomas to be about the best science writer around these days. He stated our existential problem in his own elegant style:

> We have become, in a painful, unwished-for way, nature itself. We have grown into everywhere, spreading like a new growth over the entire surface, touching and affecting every other kind of life, *incorporating* ourselves. The earth risks being eutrophied by us. We are now the dominant feature of our environment. Humans, large terrestrial metazoans, fired by energy from microbial symbionts lodged in our cells, instructed by tapes of nucleic acid stretching back to the earliest live membranes, informed by neurons essentially the same as all the other neurons on earth, sharing structures with mastodons and lichens, living off the sun, are now in charge, running the place, for better or worse.
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Where Are We Now?[1]

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IN 1974 and 1975 I had an opportunity to work with a small group of fisheries scientists towards the development of a series of reports that were intended to constitute an overview of the "state" of fisheries science in Canada. The result of my participation, a mixture of some science and some "gut reactions," was published along with others as a "Perspective" by the *Journal of the Fisheries Research Board of Canada* (JFRBC) in 1976 (33: 1822) and bore the title: "Science for Canada's Fisheries Rehabilitation Needs." Part of that paper was really a confession that this freshwater fish manager had not read nor thought about what had been written about the concept of "stocks" in Pacific salmon until that time. The paper documented my initial recognition of apparent similarities between what was understood about stocks of Pacific salmon and what was understood about some of the freshwater species such as lake trout (*Salvelinus namaycush*), whitefishes, walleye (*Stizostedion vitreum vitreum*), etc. The paper then documented some of the concerns which, for me, emerged from this different way of looking at what was known about freshwater fish; concerns about the implications of the stock concept to freshwater fisheries management practices generally, and to fisheries rehabilitation in particular. Those concerns, but not much wisdom or insight, have since been transmitted to the fisheries agencies with which I have been associated; the Ontario Ministry of Natural Resources, and the Great Lakes Fishery Commission.

I have related this little story, not just because it has something to do with STOCS, but because as a typical, busy, fisheries manager, I had not been looking at science available if it had no obvious connection with my own immediate areas of interest. I learned some things important to my job in the process of looking outside my own arbitrary or habitual area. That experience is typical of fisheries managers, and I will be bold enough to say it is also typical, though perhaps to a lesser degree, of fisheries researchers.

This little story explains, in part, why the Great Lakes Fishery Commission is the lead sponsor of this symposium, and my own reasons for being here to participate in the process. We need a much better understanding of the possible implications of the stock concept to freshwater species if we are to meet effectively our long-term responsibilities of managing, maintaining, and rehabilitating our natural fisheries resources in the Great Lakes, indeed throughout freshwater ecosystems.

Another experience and publication, which was the greatest and most exciting learning experience of my 30-plus years of work in fisheries, was the SCOL symposium, held in 1971, and published by JFRBC in 1972. Probably most of you know the publication, or at least some of its parts; indeed, some of you were a part of that process of science synthesis. Some of you too have been part of PERCIS and of SLIS, which were orchestrated in fashions similar to SCOL. I want to speak briefly about SCOL, and the others, because they were successful science-synthesizing exercises and learning experiences for all those involved, and they have contributed significantly to the advance of the sciences of fisheries and ecology. As such they have or will become the foundations of fisheries management programs and of new research directions which merit support. I have confidence that STOCS will emerge standing tall in this series of international symposia: It has a major scientific challenge, it has been superbly orchestrated, and it has an outstanding array of participants. Perhaps, however, it would be of some value, in collectively reaching for success in this fragile area, to look at some of the other ingredients which were and are essential. There is no audience here, only participants. Each participant is acknowledged as an expert who is volunteering his individual ingredients of experience, science, insight, and intuition to a brewing vat for 2 weeks of fermentation. I can vividly recall some personal feelings at SCOL, feelings that were felt by others far more expert than I, feelings that will be felt by some of you in the first few days of STOCS — you know the kind of feeling — "I've got this idea — or the beginning of an idea — maybe it's an insight — maybe it's a product of my ignorance — I'll keep my mouth shut and they'll think I'm a little stupid — but that's better than opening my mouth with this half-baked idea and proving I'm stupid." Let me remind you that you are recognized and selected experts whose science, insights, and intuition are needed and wanted for this rare new wine we are brewing — your ingredients, once offered, may be set aside for now, they may be used in a context other than that in which they are offered, but none will be rejected — all are needed. It's not at all like it is back home — where one is expected to be, or feels he is expected to be, an authority and to be right. In this STOCS symposium, as in SCOL and the others, we offer, we think, we sift and test, we synthesize, we brew, and we all learn. Those who offer most learn most.

This bit of chatter, you will recognize as an admonition that you try to be open with your ideas, half-baked or otherwise, because there will be no personal criticism and because it's part of the learning experience and part of the process of advancing and synthesizing our science, and our personal perception of our science. That line — about the more we offer, the more we learn — can't be entirely logical, because I learned far more in SCOL than I offered. However, it works as a generalization.

And now, having rambled through a couple of personal experiences which I thought might be helpful as we begin our attempt to synthesize and expand our understanding of another segment of fisheries science, the focus this time being "the stock concept," I return to my topic — "Where are we

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now''? I have not been able to develop a consensus statement for managers in general about what we understand or don't understand about the stock concept and its implications for freshwater fisheries management. I have a feeling that a consensus reaction to any pointed question would be a considerable bit of foot shuffling, followed by a defensive monologue designed to change the subject to a more comfortable area. I must therefore submit my personal understanding, or lack of it, as an indication of one manager's present perception of the state of this part of the science. You may already have read that perception in my 1976 paper; my perception has changed little since that time.

I'm still not comfortable with the several ways of defining the operative differences between stocks of fish within a population. I think it has something to do with adaptation to specific sites such that natural reproduction is successful. With a consensus on the definition, we would all be talking about the same thing. Please develop, if you can, a definition which can be meaningful in management.

I still don't know if the stock concept is peculiar to Pacific salmon, or whether it is also a characteristic of freshwater fish and other fish species. Life for a freshwater fisheries manager would be much simpler if the answer is that it is not a consideration for freshwater fish management; but if the answer is yes, then we should get on with facing it and with making the necessary changes in what we are doing. I don't think that any serious fisheries manager believes he is doing a real job of natural resource management, or is doing more than creating fishing opportunities in the short term, by means of the current massive salmonid plantings characteristic of the Great Lakes and some other locations in Canada and the United States. That such practices should be popular with some of our clients is not surprising — it is perceived that someone else pays for it. Contrary to what is presented by some managers as success stories of fisheries management based on a breakthrough in our fish culture technology, the results are not new to fish culture; they are happening because our environmental mismanagement has created the situation for ''success'' which would have been denied, as in former years, had we been able to manage successfully the quality of our aquatic environment. Note also that while we create fishing opportunities, we still reach for natural reproduction by the fish we plant.

Are we with our fish culture programs disrupting successful natural reproduction by groups or stocks of fish that have become adapted to local sites? How can we select stocks of fish which are likely to reproduce successfully naturally in specific locations? Do we need to make such selections?

In the recent past, fisheries science has been such as to push fisheries people to the fore, the frontier of ecological thinking, and to a leadership role in environmental management. It is important that we continue to provide that kind of leadership to society, uncomfortable though it may be, until some other profession merits the role. Your deliberations in STOCS will provide part of the basis for our ability to continue to provide that leadership, and help us to avoid falling into the passive role of expedient engineering-like response to current situations.

As you address the issues presented to you in this symposium, you are not only addressing issues of immediate concern to fisheries managers and to clients of fisheries managers and researchers, you are addressing questions of ecological significance to society at large.

I wish you, us, success. Thank you.

Changing Management of Great Lakes Fish Stocks[1]

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DURING the next few days I expect that we will talk at length about how things should be. And that is good and very helpful in setting goals and objectives for management. But in our case, as it is so often, what should be is a far cry from what is. Today, during the next few minutes, I will speak about what is. That, too, is important. We need to take stock of where we are in relationship to where we are going to chart our journey realistically. I will speak from Michigan's perspective as owners and managers of 41% of the Great Lakes, and I will speak chiefly of the upper three lakes, Superior, Michigan, and Huron, of which we manage 64%. I will discuss briefly the current management status of several interesting and important species, and I will then discuss the status of management per se. I hope that my remarks will make it clear that we are managing unstable fish stocks of frightening importance in only the grossest of terms right now.

In the past 15 years, Great Lakes fish populations have been rebuilt from catastrophe. There were few survivors of the three bombs that exploded in mid-century — overfishing, lamprey, and alewife (*Alosa pseudoharengus*). Should we add to that the insidious effects of chemical warfare, it is little wonder that today's fish stocks bear little resemblance to anything that went before. The strong, self-sustaining populations of lake trout (*Salvelinus namaycush*) and coregonids are gone. In their place are hatchery-supported lake trout, Pacific salmon, alewife, smelt, and a much subdued coregonid assemblage. But the fish assemblage is not the only change, perhaps not even the major one. Commercial fisheries have suffered setbacks from which they will never fully recover, and in little more than a decade, a sportfishing economy worth hundreds of millions of dollars has sprung up around the new Pacific salmon and lake trout abundances. Those abundances stem not only from stocking, but from a seemingly endless supply of prey.

Rainbow smelt (*Osmerus mordax*) and alewife (*A. pseudoharengus*) in one way or another form the key to the abundance, growth, and survival of many Great Lakes species. They comprise over 90% of Lake Michigan's biomass. Their high levels of abundance are suspected of having negatively impacted coregonid chubs, lake herring (*Coregonus artedii*), perch, walleye (*Stizostedion vitreum vitreum*), whitefish, and emerald shiner (*Notropis atherinoides*).

Recent periods of relatively low abundance of alewife in Lake Michigan have apparently resulted in reduced growth rates and survival of predator species such as salmon, steelhead, and lake trout.

Because salmon, steelhead, lake trout, and other salmonids have such overriding economic importance in all of the lakes except Lake Erie, it is important to balance salmonid stocking with their principal prey. Overstocking of salmonids could cause collapse of either or both of these prey species with disastrous results to the salmonid sport fishery.

Poor growth rates of Lake Michigan coho salmon (*Oncorhynchus kisutch*) in 1979, which followed a downward trend in growth rates spanning several years, strongly suggests that salmonid stocking rates in Lake Michigan should be increased no further. Coho growth rates in 1980 were substantially improved as a result of improved alewife abundance, but that may be only a temporary fluctuation common to stressed systems.

Another Pacific salmon, pink salmon (*O. gorbuscha*), only a curiosity a few short years ago, are expanding their numbers and range at an astounding, if not alarming, rate entirely through natural reproduction. About 20 000 pink salmon were accidentally introduced in the Current River, Ontario, in 1956. We estimate that Lake Superior's spawning run was around 100 000 in 1979, up by nearly an order of magnitude over the 1977 run. Many new streams attracted spawning runs last year and pink salmon were recorded in all five Great Lakes.

In hopes of controlling pink salmon until more is known about them, we intend to allow commercial harvest of pink salmon in and around the mouths of spawning streams. But we fear that our commercial fishermen may not show much enthusiasm. The runs of pink salmon are of short duration and are scattered in hundreds of small, inaccessible streams. Pink salmon are small, about $\frac{1}{2}$ kg each, and besides having the poorest flesh quality of all the salmon, they deteriorate very rapidly in quality once the spawning cycle begins. They offer little attraction to sportfishermen.

In Lake Michigan, bloater (*C. hoyi*), the only remaining chub species in any abundance at all (four others have become all but extinct in the past three decades), shows strong signs of life. Two very strong year-classes in succession, after several years of meager reproduction and steady decline, have managers planning for increased commercial harvest even though deep-water stocks remain at low levels and are cause for concern. Chemical contaminants, unfortunately, will keep southern Lake Michigan chubs from the market for some time regardless of their abundance.

Lake herring, *C. artedii*, once abundant throughout the lakes, is now at very low levels in Lake Superior, in northern Lake Huron, and in Grand Traverse Bay of Lake Michigan. Except as an incidental catch, herring have been off limits to commercial harvest since 1976, but no encouraging population response has been noted. Heavy commercial exploitation may have driven this species below some critical level of abundance. Based on segregation during spawning and morphological differences, it appears that two separate stocks exist in Lake Superior.

Lake whitefish, *C. clupeaformis*, yields from Michigan's waters of Lakes Huron, Michigan, and Superior have rapidly recovered to modern-day record levels in response to com-

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mercial fishing controls. Unfortunately, Michigan's expanding Indian gillnet fishery threatens recent progress. Attempts are being made to identify discrete stocks of whitefish in Lake Michigan through tagging studies. We assume, because of differences in growth and survival rates of whitefish between management areas on Lake Superior, that we are managing separate stocks, but for the most part, our whitefish management is still at the species and area level. Whitefish are protected at spawning time, which is a good hedge against excessive exploitation of individual stocks when they are concentrated and vulnerable.

Yellow perch (*Perca flavescens*) abundance has shrunk since alewife invasion into the upper Great Lakes. Although commercial production remains high in Green Bay and Saginaw Bay, abundance in the main bodies of the lakes is down and populations show no signs of returning to pre-alewife levels. Michigan allows no commercial perch harvest outside of Saginaw Bay. Again, management is by area rather than by stock.

In the case of walleye (*S. vitreum vitreum*), Michigan has allocated all harvest to the sportfishery. Like perch, walleye abundance seems to have suffered from alewife competition in the upper lakes. Walleye stocks in the upper lakes remain healthy only in the connecting waters of northern and southern Lake Huron. By way of contrast, walleye are now flourishing in western Lake Erie in response to quota management. River spawning runs are protected by closed seasons in Michigan. Midsummer stocking of pond-reared walleye fingerlings averaging 2–3 in. (1 in. = 25.4 mm) in length has produced excellent results in Little Bay de Noc, Saginaw Bay, and at the mouth of the Muskegon River. An excellent walleye sportfishery is being sustained in Little Bay de Noc through the stocking of only 120 000 fingerlings annually.

Muskellunge (*Esox masquinongy*) and smallmouth bass (*Micropterus dolomieui*) are locally important game fish of limited distribution and abundance dictated by habitat. Michigan's muskellunge population is, for all practical purposes, limited to Lake St. Clair. Michigan has a 38-in. size limit on muskellunge and a closed season that protects stocks congregated for spawning. Similarly, smallmouth bass are protected until after vulnerable spawning populations disperse. A 12-in. size limit protects them after that.

Lake sturgeon (*Acipenser fulvescens*) populations, once very abundant in the upper lakes, were long ago brought to very low levels through commercial fishing. Construction of dams on major spawning tributaries has contributed to their decline. Their numbers appear to be rallying somewhat in response to relatively recent protection from commercial exploitation (since the mid-1960's in Michigan). The species is now quite common in the St. Clair and Detroit rivers and in the Menominee River, and a few are found during spawning migrations in several of our large tributaries to northern Lakes Michigan, Huron, and Superior. A sizable landlocked population exists in the Cheboygan River system of northern lower Michigan. No effort is being made to identify or manage discrete stocks.

Lake trout (*S. namaycush*) was the dominant predator of the upper Great Lakes prior to the sea lamprey invasion of the 1940's and 1950's. Their near extinction precipitated the formation of the Great Lakes Fishery Commission and a massive international effort of lamprey control and lake trout restocking. Abundance in the upper Great Lakes is now largely reflective of annual stocking that began on Lake Superior in 1958, Lake Michigan in 1965, and Lake Huron in 1970.

Naturally produced lake trout constitute a significant part of the lake trout population only in Lake Superior and, in particular, western Lake Superior where some native stocks survived lamprey predation through to the time of initiation of lamprey control measures. In much of Lake Superior and in the other lakes, restoration of self-sustaining stocks has been agonizingly slow. There has been much talk about the merits of using various strains of lake trout in the stocking program to accelerate natural reproduction, but to date, a single strain has dominated rehabilitation efforts. It appears likely, judging from the present management attitude, that other strains may be introduced within the next few years in an attempt to accelerate restoration of self-sustaining stocks.

As mentioned earlier, present lake trout stocks support excellent sportfishing of great economic significance. But commercial fishing for lake trout has not been satisfactorily restored for a number of reasons, not the least of which has been chemical contamination in excess of Federal Food and Drug standards for human consumption. Some incidental catch does occur, however, and in the last few years, Indian fishermen have taken increasingly large numbers of lake trout from Michigan's waters. This unregulated Indian gillnet fishery has depleted stocked lake trout in sizable areas of northern Lakes Michigan and Huron and in parts of Lake Superior and created new management headaches where none were needed.

Sea-run rainbow trout (steelhead) (*Salmo gairdneri*) were introduced into the Great Lakes in 1876. Nearly all early introductions stemmed from the McCloud River strain in California and although other strains have since been introduced, it is safe to say that the existing migratory steelhead population in the Great Lakes has evolved from that strain. Roughly one-third of Michigan's steelhead are a product of self-sustaining stocks. Most state agencies, including Michigan, stock hatchery-reared steelhead in streams having inadequate natural reproduction to support sportfishing. Eggs for stocking purposes have come largely from Michigan's Little Manistee River. To maintain the desirable characteristics of the Little Manistee River run, preferred fall migrants receive considerably more regulatory protection than do spring-run fish. To maintain the wild characteristics of the stock, no hatchery-reared steelhead are planted in the Little Manistee.

Steelhead have apparently made some adjustments to our heavy runs of coho and fall chinook. Our once popular September steelhead fishing has declined since Pacific salmon were introduced in the mid-1960's. Fall steelhead now seem to delay entering parent streams until after the salmon run (mid- to late October). I suspect this is behavioral but all I can offer now is the observation that the character of our fall steelhead runs has changed, seemingly in response to the Pacific salmon introduction.

Coho salmon and chinook salmon (*O. tshawytscha*) were successfully introduced in the upper Great Lakes in the mid-1960's. Although both of these species have established modest self-sustaining populations in numerous tributary streams, population levels in these lakes stem almost entirely from hatchery stocking. These two species are the dominant predators in Lake Michigan and they support an extremely

important sportfishery there and in Lake Huron where they share dominance with lake trout. Their growth rates are comparable to ocean salmon. The world record coho, a 39-lb (1 lb = 0.453 592 37 kg) 2-oz (1 oz = 28.349 523 g) specimen was taken from Michigan in 1973. Chinook of 25–30 lb were quite common in the 1980 Lake Michigan sportfishery.

The egg take that supports Michigan's salmon stocking program and much of that of other agencies comes from Michigan's Little Manistee and Platte rivers. We have been selecting eggs from early running coho from the Platte because experience indicates that they provide the best open-water fishery. Weather conditions for fishing deteriorate after early September on the lakes. Thus, prespawning concentrations of coho are more efficiently harvested if they occur before the onset of unsettled fall weather.

In the case of chinook, preference is given to large specimens during the egg take and diseased and deformed fish are avoided. Other than that, little attention is paid to stock management. In spite of this, most observers will admit that the quality of chinook salmon fishing has shown a clear upward trend since its introduction.

Michigan has been experimenting with Atlantic salmon (*Salmo salar*), but stocking rates have been low. The few that have been caught are well received by sportsmen and it is quite possible that increased hatchery production of Atlantic or landlocked salmon will allow us to increase levels of this species in the lakes. A 30-lb 12-oz salmon was caught from Lake Michigan this summer.

That is a brief rundown of the status of Michigan's Great Lakes management from a species standpoint. Clearly, the fish populations and fisheries of the upper lakes are still very much in a state of adjustment and many challenges to management lie before us. These future challenges must be met with unflagging enthusiasm.

Although we in Michigan have had considerable success with stocked salmonids in a nearly ideal media, Michigan's overall data base for management is uncomfortably thin. We are not getting the catch data from either the sport or commercial fisheries in the detail we need. The analysis of the data we do get is inadequate. Survey data and actual observations on community dynamics and species behavior are pathetically weak. It is our goal to build our strength in these areas, but until we do, we invite management mistakes. Perhaps not the mistakes of the past because it is hard to imagine such calamity recurring, but expensive mistakes just the same. Also, Michigan is not alone in its anxiety; other agencies responsible for a segment of Great Lakes fisheries management are in it with us.

We managers are expected to maintain an optimum flow of benefits from a staggeringly valuable and complex resource to an equally complex clientelle with scant knowledge of either. It's no wonder we are anxious. Being here at this symposium is a rare opportunity for my fellow managers and for me. It is a time for us to reflect upon the findings of research and indulge in some of the finer points of management. We need and relish opportunities like this. I can't help feeling, though, that we take from these meetings more than we give. For that, I thank you all in advance.

A Perspective on Population Genetics and Salmon Management[1]

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THERE is an apocryphal Chinese proverb to the effect that, if you bend over backwards far enough, you may as well fall on your face, and this is the text for the following anti-keynote sermon. It seems to me that the major thrust of this conference is to so thoroughly intimidate all prospective fish culturists, that they will desist from any but the most expensive, research-oriented kinds of operations until a whole new science of fish population genetics has been mastered. I view this thrust as unrealistic, and as an alternative suggest what seems to be a more practical and enlightened course of action for the next two decades. Having begun by stating my conclusion, it now only remains to reconstruct the painful logic that leads to it. My remarks are primarily addressed to Pacific salmon fisheries on the west coast of Canada, but may also be appropriate to the Great Lakes as well as to a variety of other fisheries.

Pacific Salmon Fisheries — Their Management Today

Pacific salmon, like other salmonids, are characterized by a marked tendency to return as adults to their streams of origin. In consequence, their many populations are subject to various degrees of isolation, which presumably, in part, reflect some degree of adaptation to their local environment. For this reason, it has long been a premise of management that each population should be harvested separately. Much of the complication of Pacific salmon management stems from the difficulty of harvesting each population separately when the various populations intermingle during their inshore adult migrations. The intermingling of salmon from various streams is only a coarse approximation of the mixing problem, for the various tributaries of a river may each have separate populations and within each tributary there may be subdivisions related to timing. It could well be that the differences among the tributaries of a single river are greater than those among comparable tributaries of different rivers. It is as though salmon of a particular species, say sockeye salmon (*Oncorhynchus nerka*), have the inherent capacity to diversify over the range of environments that a river system presents.

The differences must be considered in management. Suppose that all salmon of a single species returned to their home streams but were not divided into distinctive stocks. Then a common rate of harvest applied over the whole coast for the whole season would, on the average, be acceptable. However, the varying effects of environmental factors would require varying the rates of harvest for different streams from year to year, and there would still be common harvesting of the several species. These problems are compounded further by the individual characteristics of the many stocks of each species. If two populations are unequally productive of recruits from equal populations of spawning adults, then a common rate of harvesting will affect them differentially (Ricker 1958; Paulik et al. 1967). If two populations have a different average size at the age of return, a gillnet fishery with a particular sized mesh will harvest them selectively (for example, Todd and Larkin 1971). If there is a difference in timing between stocks, the economics of the fishery may concentrate the harvest on the earlier stock (Hartman and Raleigh 1964).

Underlying all these complications of harvesting is the assumption that if the populations could be sorted out and then harvested individually without any selection (i.e. if those caught were taken at random), it would be possible to achieve a maximum sustainable yield and maintain genetic composition. All populations might not conform to the same mathematical model in their stock–recruit relation, but all would exhibit some optimum escapement that would maximize the catchable surplus.

It is against this broad biological background that salmon managers pursue their goals. Given their "druthers," they would probably express a preference for harvesting fish on the spawning grounds; but since the value of the salmon as food is low there, it is necessary to put up with a fishery that occurs earlier and that inevitably involves more admixture of stocks. The fact that salmon must be taken at sea also creates more uncertainty about the number of fish that should be caught. The estimation of the size of a returning adult population is usually based on a variety of bits of information, the most useful usually being the catch rate of incoming fish in the commercial fishery. The manager almost invariably has only a rough idea of how many are coming in. Because the prime concern is to ensure the optimum number on the spawning grounds, there is often an effort to measure escapement from the fishery directly with a fence, or indirectly with a test fishery if practical, and at least with a guess from a stream survey on the ground. One way or another, the manager does the best he can to achieve optimum escapements of each of the stocks.

The whole exercise is obfuscated by social and economic considerations. There are various "clubs" of commercial fishermen that are organized by the kind of fishing gear they use, and there are sport fishermen; management must consider how to divide the catch. There are also matters of social convenience that dictate weekly divisions of the season, each of which begins at 18:00 Sunday with the opening of the fishery. As well, there are international agreements and disagreements, and native Indian rights. In these several circumstances, there are many ways for the manager to err, the greatest sin being to let more than the estimated optimum number of salmon spawn. As might be expected, the fishery is not managed to perfection, and there is frequent resort to excuses and hindsight explanations for what was done in the

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hurly–burly of the fast-moving fishery. In recent years the power of the fishing fleet has been so great that in each week, only 1 or 2 d of fishing can be allowed. As a result, imperfections in management have become greater.

Over the several decades that the Pacific salmon fisheries have been managed intensively, there has also been a steady change in the environment of many stocks of salmon. The details are familiar and tedious to relate. It will suffice to say that the capacity of many river systems to support salmon populations is much less than it once was. There is, nowadays, a greater awareness of these effects, and to some extent the worst abuses are now less likely to occur. Nevertheless, the attrition of environments continues, and there is every prospect that it will neither cease nor be reversed.

The obvious way to compensate for the shortcomings in managing the fishery, and of offsetting the environmental degradation, is to give the fish a helping hand by a variety of techniques that are called "salmonid enhancement." Dr. A. W. H. Needler once remarked that the word "enhancement" is a poor choice to describe the main thrust of these activities, for the object is not to improve upon salmon. Loftus (1976) made much the same point in his extensive discussion of the subject. Properly viewed, so-called "enhancement" should be labeled as "restoration" or "rehabilitation" insofar as techniques are aimed at patching up damage, and "augmentation" as they may improve upon natural production. The removal of obstructions to migration, increasing minimum stream flows by water storage, diverting wayward stream channels, constructing artificial spawning streams, lake and stream fertilization, egg-rearing boxes, and many such techniques are all essentially restorative or augmentative in nature.

The techniques of hatchery culture may intrude more into salmon biology and may offer some hope of improving on salmon, literally enhancing them. This was certainly among the aspirations of the early salmon culturists, and great hardships were endured to get eggs and milt from exotic sources where the fish were larger than elsewhere. Similarly, most hatchery operations practised some measure of genetic witchcraft, selecting particular fish as parents, and particular offspring by the rearing and sorting techniques. Much of the selection was inadvertent and no doubt preserved some fish, at least until the time of release, that would not have survived naturally.

Modern hatchery managers are much less prone to do private experiments, and the regime of operation is more stereotyped. The prevailing belief is that selective effects should be minimized. The parents should be randomly chosen or should at least be chosen haphazardly. Rearing procedures should not knowingly be selective, unless to indicate what kind of procedures might be desirable to achieve preservation of genetic variability. The objective of modern salmon hatchery practice is to produce the maximum number of returning adults, leaving selection alone except as it happens as a combination of inadvertence and nature.

Of more direct concern to managers is the joint harvesting of hatchery and wild stocks. If the hatchery is even modestly successful, the rates of harvest it will sustain may be much higher than those of wild stocks. Unless the hatchery salmon are harvested at the "hatchery gate," there will almost certainly be an over harvest of wild stocks, especially those of the stream on the banks of which the hatchery stands. Such considerations prompt some of the current nightmares of salmon managers.

To summarize, contemporary salmon managers are a beleaguered lot. They are dedicated to some commendable ideals of salmon management, but it is difficult to achieve maximum sustainable yield and demonstrable genetic stability when several thousand stocks are harvested, in part together, by a fishery that is much more powerful than need be, and for which efforts to compensate for the mistakes along the way may be fraught with unhappy consequences. Most contemporary salmon managers are ready to admit privately that what they are trying to do is, for all practical purposes, impossible. To collect and analyze rapidly all of the relevant data on all of the stocks in each week of the fishery is technologically conceivable, but the cost would dissipate much, if not all, of the revenue of the resource. The remaining revenue would certainly be used up in the necessary enforcement of regulations, surveillance of spawning grounds, and implementation of restorative measures. Salmon management is in a cul de sac of frustration.

Thoreau to the Rescue

The quotation of Thoreau that is most memorable (and most readily remembered) is "simplify, simplify, simplify" and it suggests at least one way of resolving some of the problems of the salmon fisheries. Consider, for example, the matter of the regulation of the fishery. It has many times been suggested that the total harvest of salmon could be taken with perhaps a dozen large traps plus a small fleet for mopping up operations. Unfortunately, that kind of simplification is not socially acceptable, so what has been attempted has been to cut down the size of the fleet by a licence limitation and buy-back scheme. This has not been successful, for the decline in numbers of vessels has been more than offset by an increase in average catching power. At the same time, the sport fishery has increased substantially. What is needed is a kind of simplification that will do almost as good a job of regulating catch as is now done; that will minimize harvesting of mixed stocks; that is cheaply and effectively administered; and that may, through ordinary economic processes, lead gradually to a decrease in the size of the fleet. For example, concentrating fishing in so-called "terminal" areas close to river mouths and permitting fishing for only 1 d a week for all kinds of commercial gear (except trollers, which should be banned) on a coastwide and season length basis, would probably do a better job of regulation in lean years than at present, with much more convenience in enforcement and much less need for manipulation of statistics. The same technique would probably not be acceptable for regulating sport fisherman catches, and some form of seasonal bag limits coupled with outright short-term closures are probably preferable. The details are highly technical: suffice it to say that simplification in regulation is highly desirable.

The effort saved in regulation should probably be diverted to more intensive work in restoration and augmentation — patching up mistakes and increasing natural opportunities for production. As an alternative to intensive and complex regulation, this kind of activity is probably more cost effective. This brings me to a second example of how to apply Thoreau's injunction to "simplify, simplify, simplify." The

simplest, safest, and most lasting ways of assisting salmon populations are highly localized. They require an intimate knowledge of a stream, close scrutiny of its ecology, and attention to many geographic details. They are, perforce, labor intensive.

Unfortunately, there is a widespread conviction among Canadians that there are already too many public servants, and it is accordingly difficult to mount salmon enhancement measures that require field staff.[2] But there can be little doubt that one of the best ways of maintaining salmon populations is to put a large number of people into the field to work at the fine-grained structure of salmon production.

But How About Hatcheries?

It is partly for the reason that manpower is politically limited, and partly for the reason that there are imagined economies of scale, that much of the effort in "enhancement" programs is invested in large-scale centralized hatchery operations. There is abundant precedent for large-scale hatchery construction in the United States. With new technologies for rearing fish and great pressures for increased production, the attraction of big and apparently efficient structures was irresistible. But the history of these establishments has been chequered, and serious doubts have arisen concerning their effectiveness.

Aside from the reality that large-scale hatcheries literally put all one's eggs in one basket, with all that is implied about risk taking, they create an environment for potentially large-scale genetic interference with salmon populations. Operations which hold coho salmon (*O. kisutch*), chinook salmon (*O. tshawytscha*) and steelhead trout (sea-run rainbow trout) (*Salmo gairdneri*) for periods of up to a year or more are the most common today. The typical scenario for this kind of operation anticipates that selection, both conscious and inadvertent, reduces genetic variability, rendering the population less fit to cope with environmental vicissitudes and less able to exploit the diversity of natural environments (see, for example, Thorpe 1980).

In some measure this seems a plausible conjecture, especially if there is some deliberate selection for fish with particular characteristics (say a brood stock). But there are many other potential aspects of hatchery selection to consider. By increasing survival to seaward migration by an order of magnitude, hatcheries may, at least in their first years of operation, simulate the sort of success associated with early colonization of a new environment. Young salmon that would not otherwise survive to become adults will do so. It might be expected that average age of return would be reduced, for in 6 years, two generations of 3-yr-olds will produce a much larger population than one generation of 6-yr-olds. If colonization is the name of the game, short generation time is important.

It is also to be borne in mind that there is a great difference in the densities of fish in hatcheries as contrasted to natural environments. There are good grounds for expecting behavioral and physiological conditioning that may subsequently be reflected in survival after release. For example, it is alleged that coho from hatcheries are prone to school at sea, and are more frequently caught in bunches than their wild counterparts (Matthews personal communication). It is becoming commonplace to look for physiological signs of stress in hatchery fish (Wedemeyer and Yasutake 1978). It has also to be borne in mind that hatcheries create artificial environments with respect to nutrition and disease, and the failures of many earlier hatchery plantings were a frequent reflection of poor feeding practices, or the ravages of infectious diseases. Today's practices are more informed, but are also nevertheless nonnatural.

All of these characteristics of hatchery culture must be reckoned with, both in their short-term effects and in their long-term genetic implications. Moreoever, straying to environments other than the home streams may also be characteristic of some of the strains that flourish in hatchery environments (see, for example, Simon 1972). It also seems possible that the straying of hatchery fish may reflect the circumstances under which they are reared, instead of, or perhaps in addition to, their genetic makeup. In any case, hatcheries may contribute to genetic effects both in the population with which they are directly concerned, and other populations far distant.

There are also ecological impacts of hatchery practices. The high densities of fish in the hatchery may be followed by unnaturally high densities for a period after release which may result in displacement of wild fish and unusual dispersal of both wild and hatchery fish. This may also be followed by similar reverberations in estuaries and offshore rearing areas, especially if the various stocks of the various species are, in natural circumstances, involved in partitioning of the temporal and spatial grazing resources of the sea.

In these contexts, hatchery practices may have wide and various effects, many of which, because they are conjectured, are usually viewed as bad until demonstrated to be otherwise. The obvious moral is not to build large and centralized hatchery facilities. This was made clear at the outset of the Salmonid Enhancement Program (for example, see Larkin 1974). For a variety of reasons, the expenditures in the first 5 years of the program have gone disproportionately to large-scale hatcheries.

Some Room for Hope

It is rather surprising that there is currently no explicit working hypothesis of population genetics in the salmon management kit box. Ricker (1972) summarized the available literature and demonstrated convincingly that the observed differences between stocks were both hereditary and environmental in origin, but he did not draw any morals for management. Loftus (1976) took the view that all stocks should be preserved if possible, and Larkin (1979) took much the same conservative attitude. The implied working hypothesis is that genetic variability should be retained, and all meddling with genetics should be minimized. This is a view that needs challenging, for life is probably not that simple.

For example, we have passively accepted the idea that populations which are producing a maximum sustainable yield should have the same genetic characteristics as those which are unharvested. This idea seems to come from the belief that, in a natural state, populations exploit the greatest

[2]Recourse is taken to various contracting devices to provide manpower that is less visible, but these arrangements are neither adequately systematized nor coordinated.

number of opportunities that are available and thereby maximize their abundance. It is important to appreciate that maximizing abundance is not the same thing as maximizing catchable surplus (for a recent theoretical discussion that is highly relevant, see Caswell 1980). Perhaps instead of asking, what we can do to preserve natural genetic variability, we should ask, "What genetic characteristics should we attempt to foster to increase the permissible and sustainable catch?"

This may prove to be a difficult question to answer, particularly because the technique of the fishery may be limiting. But first suppose that the fishery was on the spawning grounds and could be made to conform to any pattern desired. The fish should probably not be taken at random, but how should they be taken? The answer is probably different for the various species. For pink salmon (*O. gorbuscha*), which are almost exclusively 2 yr old at maturity, it might seem reasonable to catch the smaller ones. For chinook it might be argued that it is best to harvest the larger ones that stay longest at sea, if the added years at sea do not increase biomass sufficiently to compensate for the longer generation time. The same might be said for sockeye that spend an extra year at sea. But that might interfere with the genetic interplay of, say, 5-yr-olds and 4-yr-olds as well as change the population dynamics in the rearing lake, leading to cyclical dominance characteristics (see, for example, Larkin 1971). There is also the possibility that sustained fishing on seagoing sockeye would lead to a preponderance of residuals that would never go to sea, a possibility once mentioned by McCart (1971), from which the inference would be to harvest residuals in the lake to maintain interest in going to sea.

When the realities of the selectivity of the fishery are added as an additional factor, one is faced with a much more complex situation. Gill nets may usually select larger (and older) sockeye, but in a year when all sockeye are larger, may select the smaller ones (Todd and Larkin 1971). Gillnet selection of larger pink salmon is probably more invariable because more mesh is hung, and has led to production of smaller fish (Ricker et al. 1978). Troll fisheries on chinook salmon stocks that are close in to the coast for several years automatically select against fish which are older at maturity (Ricker 1980). Many more examples could be cited, but they all serve to underline that the fishery is selective now and in a complex way. For the future, we need to know not just how the fishery is selective, but what the consequences are, and how the fish should be selected to achieve the desired results of maximum sustainable yield.

Bearing in mind that it will take a long time to gain that understanding, it does not seem unreasonable to consider various enhancement practices, particularly hatcheries, as an opportunity to offset selective effects of the fishery. Where a fishery selects larger, older, or earlier fish, these should be given the benefit of enhancement measures. In our present state of knowledge we may not be entirely successful in attempts either to offset the selective effects of the fishery, or to select the best characteristics for maximum sustained yield, but the alternative of doing nothing to manipulate the genetic machinery is probably much less satisfactory as a response to the present situation.

A second consideration is that the necessary population size for retaining the characteristics of a stock virtually indefinitely is almost certainly very small, unless fish are very different from other animals. One hundred individuals should be enough (Falconer 1964, p. 68 et sequentia). Where there is a large preponderance of one sex, as is the case for chinook salmon, it may be necessary to have, say, at least 50 females. This is reassuring, for it means that even small remnants of stocks can be used for rebuilding. Insofar as genetics is concerned, we should not become too hysterical about population declines to low levels.

Third, we should remember that many, if not all, stocks may retain the potential for colonizing, which they obviously must have had to become established in the first instance. The history of transplants from one stream to another has not been encouraging, especially when the donor streams were far distant from the receiving waters. Nevertheless, some long distance transplants have been successful, to which the Great Lakes and New Zealand bear witness, the former for pink and coho and the latter for chinook. On a more local geographic scale, transplanting has almost invariably resulted in lower survival to maturity, and has commonly produced a considerable amount of straying to streams other than the donor stream (Ricker 1972). Many of the disappointing results of transplants may be explained by a wide difference in the characteristics of the donor and recipient streams (for example, Cultus Lake sockeye from a coastal setting to Eagle River on Shuswap Lake in the interior of British Columbia). Other disappointments may reflect the timing of releases, the history of rearing in a hatchery, the effects of marking, and so on. Considering the many things that could have gone wrong, it is surprising that some transplants produced any returns; but they did, demonstrating that many stocks have the potential for recolonizing other areas. Bearing in mind that altitude mimics latitude in many ways, it might be surmised that populations occupying southern streams at high altitudes may be similar to those of northern streams at low altitudes. There may be many other similar patterns that may help guide the choice of a donor stream. The recent experiments of Bams (1976) indicate that combining genetic material from the recipient stream with that of a donor stream enhances return, verifying that heredity is in some measure involved. There is certainly much more to be learned about salmon transplanting, but there is sufficient known now to encourage the view that the loss of a stock from a river system is not irrevocable and should not be viewed with total despair.

A fourth consideration, related to the foregoing, is that some strains of salmon may be adapted to colonizing, at least on a limited scale; conversely, some streams may normally be occupied chiefly by strays from nearby drainages. The occupation of marginal environments at high population levels is a common theme of animal population biology (see, for example, Wolff 1980). The steady stream of colonizers to some environments is well known (see, for example, Faeth and Simberloff 1980). The existence of colonizing morphs within populations is also well known (for example, Wellington 1960).

Salmon may well show all of these characteristics. Coastal stream coho, for example, are notorious for poking their way into intermittent streams, and would appear to have spontaneously reinvaded many streams on the east coast of Vancouver Island that were dry in summer for several years after extensive logging operations in the 1930s and 1940s. Some races of sockeye of Babine Lake seem to be adapted to

a group of small streams which are similar in characteristics and may be interchangeable as "home" streams (McCart 1971).

There is also some evidence of wide adaptability of at least some strains of salmon and trout. Kokanee (land-locked sockeye) have been transplanted with success in many lakes in the interior of British Columbia. Rainbow trout (*Salmo gairdneri*) are even better known for the ease with which they are transplanted. Virtually all lakes over 1000 m in altitude in British Columbia that contain fish contain only rainbow trout that were planted at some time since 1900. Indeed, many are planted successfully every year (and not always from the same source) because there are no natural spawning facilities. Admittedly, trout transplanted to a lake may have no place to go and, in any event, are not predisposed to go to sea. But they clearly contradict the notion that there is an extraordinarily fine adjustment of all stocks to particular environments. Our belief in the almost indefinitely fine distinctions in the differences between stocks has led us to seek out differences rather than similarities, and to ascribe greater significance to the differences than is either necessary or appropriate for management purposes.

A fifth consideration is that to the extent that salmon stocks can become adapted to local conditions, it is to be expected that after an initial period of increased survival of almost all genotypes, there would be an adaptation to hatchery conditions (that is, that selection would favor the progeny of those that returned to the hatchery). A hatchery, from a salmon's perspective, may be nothing but a new stream to exploit. Curiously though, it is commonly believed that hatcheries do best for a limited span of years, and after a decade or more show much reduced rates of return. Many explanations have been put forward, the most common being to blame changing conditions downstream, in the estuary, or in the ocean. More recently, it has been considered possible that hatchery practices result in decreased genetic variability, and accordingly their effect is manifest only after a sufficient number of generations has elapsed. The theory is plausible and has some obvious inferences for hatchery practice, such as the desirability of avoiding any deliberate selection, the continued use of some wild stock for breeding purposes, the deliberate planning of a limited span of years for a hatchery operation with a particular stock, and so on.

In a related vein, there is a widespread belief that hatchery salmon may genetically dilute wild stocks by interbreeding. Much of the evidence is adduced from crosses between wild and hatchery stocks raised under hatchery conditions, for which wild × wild usually outdo wild × hatchery or hatchery × hatchery. The truth may well be that wild stocks improve hatchery strains rather than that hatchery strains dilute wild stocks, but I would even be prepared to argue that selected hatchery stocks could improve survival in wild stocks, raised in wild conditions (for example, see Moav et al. 1978).

From all these considerations, it seems appropriate to adopt a moderately optimistic attitude about stock rehabilitation with hatcheries. Recognizing that mixed fisheries on hatchery and wild stocks will affect the wild stocks should not be the reason for discouragement of large-scale hatchery operations. Instead, the facts of some degree of mixed fisheries and the value of some large hatchery operations should be accepted. In response to these inevitabilities, strong efforts should be directed to focussing hatchery-related practices to work on deliberate selection to offset selection by the fishery, aiding small residues of dwindling stocks, perfecting techniques of transplanting, identifying colonizing strains of salmon, tempering inadvertent selection related to hatchery practices by outbreeding, and by planning limited time spans for hatchery operations on stocks.

The foregoing remarks were aimed in large part at hatchery operations on coho and chinook salmon. Some further comment on sockeye salmon, chum salmon (*O. keta*) and pink salmon seems appropriate. Sockeye salmon naturally spend at least 1 year in a lake-rearing area, and the productive capacity of the lake may be limiting. Hatchery culture of sockeye has had a long history of alleged disappointment. The classic work of Foerster and Ricker (see Foerster 1968) was largely instrumental in discouraging hatchery culture of sockeye, but it is important to remember that their results were equivocal. It was not possible to demonstrate the benefits (not surprisingly in the circumstances of the fishery), but it also was not possible to demonstrate that the hatchery practices were not beneficial. As the work on Cultus Lake was done over 40 years ago, and with great advances in hatchery technology since that time, it is astonishing that the idea of a sockeye hatchery hasn't been resurrected for another trial. The phenomenal success of lake fertilization techniques may be partly responsible, but if only for the purposes of some large-scale experimentation, the construction of a sockeye hatchery now seems a worthwhile consideration as an investment for the future.

Chum salmon hatcheries already produce more pounds of catch for Japanese fishermen than of all salmon species taken by British Columbia fishermen. It is possible that this huge production may not be sustained. The number of hatcheries involved is small, they are all in a fairly concentrated area (Hokkaido), and some genetic effect may be lurking in the background. The large production of chum may be based in part on the absence of competition with other species of salmon, and in part on the ecological opportunities created by the heavy fisheries for other species of pelagic marine fishes. There may be many other reasons why the same successes are not achievable in British Columbia. But at least on a limited (but large) scale, chum hatcheries seem to be a worthy investment.

Somewhat the same may be said of pink salmon hatcheries, though there are many mysteries in the history of attempts to increase abundance and to transplant pink salmon. The challenge of creating off-year runs is as great today as it was at the turn of the century. The work of Neave (1952) clearly indicated the possibility that pink salmon populations had a small chance of establishment or rehabilitation to historic levels unless they achieved a critical and substantial level of abundance. The fact that the early life history of pink salmon is in near-shore waters, rather than in freshwater, invokes the need for understanding the dynamics of a quite different ecological complex than that of lakes or streams. The need is perhaps for some saltwater rearing facilities that will bring pink salmon to a comparable size and vitality of chum salmon hatchery releases. The work of Bams (1976) suggested the value of using some recipient genetic material for increasing returns to the home stream. The work of Donaldson and his associates has raised the possibility of producing pink salmon of age

1 and 3 to carry over genetic material to the off year. The holding of sperm for a year is another related technique that has been demonstrated (Withler personal communication). Perhaps these are only straws in the wind, but viewed constructively, they are worth vigorous experimental pursuit. Rather surprisingly, the first pursuit has been mystifying in its results. Withler (personal communication) undertook transplants involving donor stocks as controls; donor eggs and held-over (1 yr) sperm from the recipient stock as experimentals; and both raised in a hatchery in the recipient stream. There were only a few returns of fish to the commercial fishery and none to the home stream. Transplanting, it seems, is still a sort of salmon roulette, but it is worth much more attention in the future.

Some New Horizons

All of the foregoing is fairly old stuff. It suggests some opportunities for application of existing techniques without oppressive anxieties for genetic consequences. It also suggests the need for some large-scale experimentation that could yield valuable insights that will eventually bear fruit in greater production. Implicitly, I hope it contains the message that at present we are close to bending over so far backwards that we might as well fall on our collective faces. I now run the risk, if I haven't already done so, of bending over so far forward that I will fall on my face.

As never before, science is advancing explosively and there are far-reaching implications for salmon biologists and managers. In a recent speculation about the future, Larkin (1980) predicted that early in the next century we should (1) expect to be able to describe patterns of oceanic production sufficiently far ahead to calculate the mix of species and races of salmon that would yield greatest returns; (2) have solved the problem W. A. Clemens posed in the 1930s — how to culture to readiness for fertilization, eggs and sperms from salmon caught commercially; (3) understand quantitatively the genetic differences and similarities among salmon stocks, and how to exploit them to advantage; (4) understand the implications of hatchery-rearing practices and to manipulate them effectively; (5) expect that because of the foregoing we will be able to achieve maximum salmon production from the North Pacific ocean, and will accordingly be arguing about which country has what rights to which salmon-grazing resources; (6) expect to be capable of transplanting Pacific salmon to both sides of the Atlantic Ocean, and to a lesser extent to the southern hemisphere, and accordingly be engaged in controversies concerning the ecological wisdom of so doing.

Although he confessed not to be knowledgeable about molecular biology, Larkin even speculated about the staggering potentials for salmon of splicing genetic material, cloning from single cells, and the deliberate concoction of Canadian super sockeye to displace the Bristol Bay runs from the Gulf of Alaska. While all of this contains a large element of wishful thinking, coupled with some extravagances of imagination, I find myself in agreement with Larkin's line of thinking, even if I may disagree with some of the particulars. Since the above was written, Dr C. C. Lindsey has brought to my attention the work of Streisinger et al. (1981) on successful cloning of homozygous diploid zebra fish (*Brachydanio rerio*), and their speculation that the techniques might be applicable to salmonids.

These potentials and others like them are well within our grasp, if we are not intimidated by the unknown. There are things to be done now that are simple and within our capability, that would satisfy the sternest economic assessment. There are others that may involve risks, but the risks are acceptable. And there are still others that may almost certainly fail, which should be attempted on a large experimental scale. Finally, of course, there is a need for long-term research, much of which must be done at the convenience of the life history of salmon. We should be moving vigorously on all fronts if we are to achieve as we could.

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Stock Definition as a Necessary Basis for Cooperative Management of Great Lakes Fish Resources[1,2]

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Managing Today's Fisheries

THE 1970's saw perhaps as much attention given to the protection of Great Lakes fish resources as it had received in any previous decade. Heading the list of significant actions and focusing renewed interest on the lakes as irreplaceable habitat for stocks of increasingly valuable fishes was implementation in 1972 and extension in 1978 of the Canada–U.S. Water Quality Agreement. From this accord evolved a number of intergovernmental initiatives — surveillance of toxic substances, strategies for controlling phosphorus influx and dredge-spoil disposal, an "ecosystem approach" to managing the lakes per se, etc. — all calculated to repair, enhance, and protect the quality of Great Lakes waters, hence indirectly, the productivity of their fish resources.

Also meriting recognition as notable contributions to restoring and developing the Lakes' potential for producing fish, for recreation as well as food, are sustained control of the sea lamprey, stepped-up introduction of hatchery-produced predators to take advantage of flourishing (largely nonendemic) prey, and, most importantly, institution for the first time of attempts to contain directly the amount of fishing on the more valuable stocks. By now most are familiar with the binational management of Lake Erie's walleye (*Stizostedion vitreum vitreum*) fishery, the interstate oversight of Lake Michigan's bloater (*Coregonus hoyi*) chub fishery, and the state-federal administration of fisheries for lake whitefish (*C. clupeaformis*), lake trout (*Salvelinus namaycush*), and chubs in (Indian) treaty-ceded waters of the three upper lakes. As is also well known, each of these is a recent initiative, or fairly so. And none is yet functioning entirely as conceived, all being encumbered by logistical, legal, or political difficulties — some inherent, others unforeseen, most complex. But, despite their imperfections, these efforts represent a notable theme: collective appreciation by the jurisdictions responsible for protecting them that each transboundary fish stock involved is by definition limited in productivity and size. They realize further, accordingly, that the use of each must be carefully regulated lest damage result. Even more significant than joint recognition that the Lakes' fragile fishery resources are indeed finite, however, is the willingness (let alone the moral duty) of governments to cooperate in ensuring that the potential of these resources, through enforcement of annual allowable catches as perhaps the most practical means, is not impaired.

Managing today's Great Lakes fisheries thus entails, first of all, the coordinated and relentless pursuit of shared responsibility, the common discharge of which requires the best technical and at once the most practical basis for doing so. Many doubt the capacity of present fish-stock assessment and fishery management technology to provide the necessary basis. But no one can deny that mounting pressure on many of the Lakes' fishery resources — in some instances pressure actually promoted by regulatory agencies themselves — demands immediate constraint, even if the technology applied may be considered "scientifically" deficient by some of the more sophisticated and cynical among us. The luxury of more time in which to develop the ultimate in assessment technique and management strategy is one the resources cannot now afford. Whether the technique and strategy be provisional or definitive, however, one requirement remains absolutely fundamental: Each stock of interest must be definable as to its extent in space and time, and its members readily classifiable among others of the same species but different stocks as to their common lineage. The problem of classifying unit stocks of some important Great Lakes species already underlies or promises to complicate evolving plans for cooperative management of fisheries they support.

Applying Theory of Fishing

As intimated, the principle being advanced as the most efficient way to control extraction of Great Lakes fishes directly is the annual total allowable catch (TAC), or catch quota. Allocation of the TAC among jurisdictions, thence among competing user groups within them, is largely a negotiable (i.e. political) matter whose specifics need not be elaborated here. The TAC itself is a product of applying, often subjectively because of imperfect intelligence, what is commonly regarded as the modern theory of fishing.

In brief, I view this theory as that represented best in the analytical (albeit deterministic) fish-population models developed, refined, and/or exemplified by Beverton and Holt (1957), Gulland (1974), and Ricker (1975). Once the population (or stock) of interest is defined — the need for and process of definition being major considerations in themselves — estimation of its principal parameters, namely, growth, mortality, and recruitment, follows as a succession of routine, though by no means easy, exercises engaged in by fishery biologists everywhere. With the model(s) employing estimates of the parameters identified, computation of standing stocks proceeds as the penultimate step in the population-assessment process, the last one being projection of the allowable catch.

As a rough rule of thumb, I assume that the annual allowable catch of a population considered to be in maximum equilibrium is usually somewhere between 10 and 20% of the population's projected annual biomass (or total weight). By "maximum equilibrium" I mean that yearly losses do not exceed gains, while population size (overall weight) remains at whatever maximum can be accommodated, along with

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maxima of other populations, by the habitat. Accordingly, departures from maximum equilibrium dictate corresponding reductions in the allowable catch, with residual surplus production being applied to the restoration of equilibrium. One may thus infer that a practical objective of fishery management is, through limitation on catch (or control of corresponding fishing effort), to ensure restoration to, then maintenance of fished populations at, the highest level of productivity permitted by ecological circumstances, such that yields, like interest on the largest financial investment one is able to make, will be maximal.

Satisfying Basic Requirements

However straightforward in logic and simple in structure is the theory just referred to, its application as already indicated is typically difficult. Rarely is the required input statistically adequate, the desired output comfortably reliable. Basic records of total withdrawals from populations of interest, together with the kinds and amount of fishing effort involved, are commonly incomplete and often inaccurate. Essential (sample) data on the age/size/sex composition of catches (hence of populations) seem never to be sufficient in volume or representativeness. Measures of each population's incoming year-classes, or of recruitment to its fishable portion, are usually lacking. The obvious consequence of all these shortcomings is the grudging yet compelling employment of less-than-perfect data, the frequent bridging of gaps therein with educated conjecture, the introduction of more and more assumptions, and the hyperqualification of results.

But what is the alternative? Where is the better if less pragmatic formula ready to be implemented for the immediate purpose of protecting valuable resources obviously jeopardized by too heavy use? No conceivable extension of or substitution for the theory now being applied could escape many of the same input deficiencies. Though elimination of some of these weaknesses, mitigation of others, and development of more sophisticated theory may reasonably be anticipated (and should be encouraged), significant improvements are not likely soon. [In the Great Lakes applications mentioned earlier, even modest reduction of serious defects in certain data bases — e.g. unreliable and untimely statistics of recreational fishing (lake trout and walleye), inadequate data on population age structure (lake whitefish and lake trout), and poor or nonexistent information about the strength of incoming year-classes and/or annual recruitment (most species) — could quickly and greatly enhance the reliability of management references derived for fisheries needing more effective regulation.]

Notwithstanding all these considerations, however, there remains one requirement more basic as well as more elusive than all the rest. I refer, of course, to that of stock definition, which implies the certainty that fished stocks of the same species but different genotypes, physically together or apart, are not only accurately classifiable in assessment exercises but also properly differentiable in the pursuit of management programs. Inability to make the distinction where necessary — especially in the case of Great Lakes coregonids, some of whose unit stocks are doubtlessly transboundary — could unknowingly prejudice otherwise well-designed protection efforts.

Conceptualizing the Unit Stock

As is amply evident in the excellent bibliography painstakingly prepared by Gina Cunningham for our reference, the literature is replete with observations and opinions on the concept, character, and implications of something we commonly refer to as the (fish) "stock." But nowhere, insofar as I can determine, has any body of authority, as is often established to perform such functions, acclaimed a definition of it. What precisely does it mean? Where in the family of generic terms, often synonymously used — strain, race, subpopulation, breed, variety — does it fit? Apparently much uncertainty prevails, perhaps even some despair. And one can be reasonably safe in assuming there are nearly as many perceptions of what a fish stock is as there are persons professionally interested in such matters. Indeed, Royce (1972) observes that the subject (of structure in fishery resources) is "... a bewildering array of semantic problems because there is little agreement on the meaning of the words used to define groups in the hierarchy with the rank of subspecies and below...." Patently, we continue to tread on soft ground.

To be sure, my own notion of the (fish) stock has not always agreed with my fellow professionals' ideas. But over the years I have reached an accommodation with myself by adopting the term "unit stock" to connote as well as circumscribe the basic grouping on which management needs to focus attention. I have given it a definition in keeping with Cushing's (1968) but at slight variance with that of Gulland (1969). To me, a unit fish stock is one consisting of randomly interbreeding members whose genetic integrity persists whether they remain spatially and temporally isolated as a group, or whether they alternately segregate for breeding and otherwise mix freely with members of other unit stocks of the same species. It therefore represents not only an aggregation that is genetically discrete and breeds true, but also one that ultimately demands quick, easy, and accurate delineation if its innate productivity is to be most effectively protected.

Attempting Stock Definition

Such an imperative remains, of course, a technological abstraction. Despite the long and widely reiterated need to discriminate reliably among interfacing or separate unit stocks of the same species (or subspecies) as an essential requirement of theory, assessment, and management, no practical technology for satisfying it has, to my knowledge, been developed. Another look at the aforementioned (but by no means complete) bibliography will attest to this fact. Whereas numerous, many excellent, and some ingenious studies have been mounted to address the problem in one context or another, not one has resulted in the routinely applicable and acceptably reliable classification procedure either specifically sought or simply implied as the objective.

This observation reflects not so much on the skill of the researcher as it does on the formidableness of the problem addressed and the likely sophistication of the technology involved. For even where the presence of two or more unit stocks can be satisfactorily demonstrated by applying any of the definition techniques now in wide use — biochemical, immunological, serological, behavioral, morphometric, meristic, mark–recapture, electrophoretic, etc. — the routine,

postdefinition sorting thereof in subsequent assessment and management activities will likely not be feasible. Quite simply, inability to easily and cost-effectively characterize a fish's genetic makeup for purposes of quickly distinguishing unit stocks remains a major obstacle in the field of fish population dynamics.

Nevertheless, there would seem to be good reason for continuing attempts to define unit stocks wherever their existence is suspected. This is not to say, however, that the testing of such hypotheses should ever proceed with anything less than a reasonably manifest reference (probable stock), a well-conceived (survey) strategy, and the most efficient (discrimination) technique. Too many attempts at stock definition, even some undertaken to meet apparently bonafide needs (vs. others pursued solely for the sake of doing so), have failed because of one or more of the following: defective study logic, faulty survey tactics, and questionable classification procedure.

From my own observations over the years, especially during the two decades proceeding from the early 1950's when "identification of subpopulations" was perhaps more voguish than it is today, numerous studies conducted to answer questions having debatable merit come to mind. I recall, for example, an abortive attempt to check out a (contrived) hypothesis that the population of Gulf menhaden, an abundant and valuable industrial fish inhabiting the Gulf of Mexico, comprised two or more unit stocks. Study procedure merely entailed sampling the species a few times at several arbitrarily selected points across the Gulf Coast, subjecting the sample fish to a statistical analysis of their meristic and morphometric attributes, and drawing inferences from, as one would expect, the many conflicting differences detected. The result was preordained failure, owing to no previous indication, hence the flawed presumption, that the menhaden at each location represented a unit stock, any one of which could have otherwise satisfied the basic need for a study reference.

Again, I readily recount even after many years a very costly exercise on the West Coast to demonstrate by mark and recapture the relative contributions of (presumed) unit stocks of Pacific salmon, by natal stream, to offshore fisheries. Here was a case of having conceptualized unit stocks based on their apparent allopatry during early and late (reproductive) stages of their life cycle, then trying to sort them out for management purposes during their quasisympatry at mid-life. Study strategy was to tag and release salmon caught systematically in the open ocean, subsequently retrieve the tags in adjacent spawning streams from the spent salmon bearing them, then extract the sought-after information from an analysis of accumulated returns. The result was inevitable failure, because the mandatory surveillance for tags on spawning and spent fish in hundreds of miles of streams during or immediately after spawning, an implicit requirement of such a strategy, was not adequately addressed or accommodated.

No further purpose would be served here by saying or speculating how many other attempts at unit-stock definition, published or not, may have been similarly afflicted. It suffices merely to assume from the wide experience already gained that such missteps will eventually diminish to inconsequence. One may be confident, too, that the process of defining unit stocks, a process whose application promises to become an increasingly necessary first step for the more effective protection of fish resources worldwide, will continue to undergo the refinement such a tool demands.

Justifying Improved Technique

Clearly, the need for well-grounded strategy applied with ever-greater precision in defining unit fish stocks is exceeded only by that for practical, real-time, and cost-effective methods of routinely and accurately classifying their members once the existence of different unit stocks is established. For maximum utility, these methods would also have to be wieldy enough for field or shipboard use, and yield results within fairly narrow limits of error. Is this too demanding and unreasonable a technological challenge? Are we forever to be denied the capability to decode and classify quickly and easily fish genotypes simply because the notion of its development is deemed unrealistic? Perhaps. But if such a challenge is not consistent with the theme and aim of this symposium, if because of its presumed insurmountability it does not merit our refocused attention, then at least a few of us will leave disappointed and unfulfilled. Moreover, as imperative as many perceive this repeatedly stated need to be, one has to wonder why the research community has yet to mount a truly serious effort to satisfy it, regardless of the seemingly awesome and overwhelming odds against complete success in doing so.

Until this long-standing technical need can be adequately met, cooperative management of transboundary Great Lakes fish populations comprising more than a single unit stock promises to be only marginally effective, even if intergovernmental regulation of fisheries based on them can be agreed to and instituted. Furthermore, unequivocal allocation of these common stocks among the jurisdictions sharing in their stewardship, let alone among the groups who vie for their use, will continue to be difficult if not legally impossible or politically impractical. One does not need to be reminded that doubts about the applicability and reliability of management references (e.g. TACs) can be expected to prevail so long as there exists uncertainty about whether unit stocks involved have been accurately defined to begin with, and their identities reliably sustained thereafter.

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The Conundrum of the Stock Concept — Are Nature and Nurture Definable in Fishery Science?[1]

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BOOKE, H. E. 1981. The conundrum of the stock concept — are nature and nurture definable in fishery science? Can. J. Fish. Aquat. Sci. 38: 1479–1480.

The definition of the word stock, as applied in fishery science, is presented in general and in precise forms. The general definition is a species group, or population, of fish that maintains and sustains itself over time in a definable area. In a more precise manner, stock (genotypic) is defined as a population of fish maintaining and sustaining Castle–Hardy–Weinberg equilibrium. If a genetic basis is not available for stock characterization, then a phenotypic stock definition has to be recognized as a population of fish maintaining characteristics which are expressed in one or more ways, depending on the type or nature of environment of domicile.

Key words: fish stocks, definition

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L'auteur définit, en termes généraux et en termes plus précis, le mot stock tel qu'appliqué à la science halieutique. En termes généraux, un stock se définit comme un groupe, ou population, d'espèces de poissons se maintenant et subsistant dans le temps dans une aire définissable. En termes plus précis, un stock (génotypique) est une population de poissons se maintenant et conservant un équilibre de Castle–Hardy–Weinberg. Si l'on ne dispose pas de fondement génétique permettant de caractériser un stock, il faut recourir à une définition phénotypique et reconnaître un stock comme une population de poissons conservant des caractéristiques qui s'expriment de une ou de plusieurs manières, selon le type ou la nature du milieu dans lequel ils vivent.

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MY purpose in this paper is to present a working definition of the word stock, as can be applied in fishery science. The definition of a stock is required because the term has been used vaguely in many ways to delimit groups of fish, from systematic (taxonomic) to applied management units. Therefore, it is difficult to establish a reasonable concept based on stock definition with quantitative measure, especially for management objectives and goals.

Murray (1961) offers a variety of meanings for the word stock, and shows that since the 14th century the biological meaning of stock has been reversed. The word figuratively means, in the biological sense, the trunk or stem of a living tree as distinguished from the root and branches. During the 14th century, stock was used to mean the source of a line of descent. The Oxford dictionary further indicates that Charles Darwin used the term to mean races that all descended from a single wild stock, and in the 20th century the word defines a related group of organisms. The term has thus been used to define what is presently called a species, and units within a species which are a race, a population, or a subpopulation.

In the late 19th and early 20th century, marine biologists began to refer to groups of sea herring, *Clupea harengus* (Heincke 1898), and various species subunits of Pacific salmon (Ricker 1972) as races or stocks based upon meristic and morphometric character distinction. Ricker (1972) has explained that fish stocks probably have genetic individuality. Many biologists have been aware of the genetic and environmental components that affect the ultimate expression, the phenotype, of a character (Taning 1952; Lindsey 1958). However, a major problem arises when one tries to distinguish between genetic and environmental, or nature versus nurture, effects on expressed characters that might be used to separate one group of fish from another. A stock of fish therefore has to be a real, measurable entity that is maintained (by com-

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pleting a life cycle) and sustained (by reproducing) if it is to be recognized and perhaps managed. Quantification of maintained and sustained characters that are genetically identifiable will alleviate the vagueness in the nature–nuture conundrum that fishery biologists face when they refer to groups of fish as stocks, and whether they are important as management units.

I face this conundrum in attempting to define a (fish) stock in terms that will permit test and hypothesis development. However, I have less problem when I define the word either generally or precisely. A general definition of a stock is a species group, or population, of fish that maintains and sustains itself over time in a definable area. This definition, though not easily quantifiable, takes into account gene flow within the stock and the exposure of these genes to time and the environment. The latter process is recognized as evolution. The genes which make up the units of living material that form individual members of fish stocks are the mainstays of evolution.

A more precise stock definition has to take into account a genetic measure that can be recognized over generation time. I therefore define a (genotypic) stock as a population of fish maintaining and sustaining Castle–Hardy–Weinberg equilibrium. A fish stock characterized by the use of the Castle–Hardy–Weinberg law would have a constant gene frequency for a particular character in each generation (Hartl 1980). There is a need to examine large samples of fish to be sure of gene frequency constancy, or of differences that would imply stock mixing. Hartl (1980), Lewontin and Cockerham (1959), and Fairbairn and Roff (1980) discuss the applications of the Castle–Hardy–Weinberg law, and the attendant problems and how they can be overcome.

If genotypic stock characterization is not possible, then a (phenotypic) stock has to be recognized and defined as a group, or population, of fish maintaining characteristics which are expressed in one or more ways depending on the type of environment of domicile. A phenotypic stock can be seen readily as one either with a color variation, a different growth rate, or any definable character difference, whether largely genetically controlled or affected in its expression by the environment.

I have stated that my stock definition should be a working definition and useful for all fish species. My genotypic definition will characterize bisexual forms, which are the majority for fish species. The act of definition is one of restriction that should permit testing and hypothesis development concerning the realities and importance of a stock to managers. If the definition is wrong, then a new data set will have to be provided for a new definition. Presumably, if natural fish variability is maintained and sustained, evolutionary units will be sustained, and resource managers will be able to apply principles of scientific fisheries management involving knowledge of stock or population homogeneity vis-a-vis recruitment, growth, and mortality. Genotypic stock recognition should prevent the pitfalls behind population or stock dynamic characterization based on data gathered from fish groups with genetic differences that are being treated as one stock by managers. For example, genetic differences in growth and maturation rates between genotypic stocks may be lost due to overharvest and a management policy that would permit it. We are not completely sure what such genetic variation losses may mean, but should we permit it?

Many questions can be asked when stock definition is quantified by means of genetic characters. We whould look at nature's genetic experiments which result in the natural distribution of fish species and ask what permits such a distribution or more specifically can fish that form the distribution be genetically characterized? Fish managers must ask, after the loss of a fish stock and when reintroduction is under consideration, whether the genetic makeup of the stock was at fault or was an unnatural environmental change imposed. What happens to the genetic structure of a fish stock when fishing mortality is imposed on regular mortality? These questions may be difficult to answer, but with a working genetic stock definition, testing and management applications could be possible.

The use of a phenotypic stock definition should not be alien to fishery managers because such a definition is largely in use today. I would argue strongly that if each phenotypic stock was managed for maintainability and sustainability, we would probably be able to maintain fish genetic variation (= heterogeneity) and the units of fish evolution. But in many cases we do not and there is evidence that managers should recognize genetic components (Moav et al. 1978) in fish stocks under management. I would prefer to consider the synergisms between management and guardianship of our fish resources. If we recognize that stock genetic variability, and measures of it, are important aspects of management, a genetic conscience can be evident in application of a genotypic or phenotypic stock concept. Nature and nurture are not separable in fish stock recognition because they are always present and interacting, and presenting a conundrum for solution.

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NOTE ADDED IN PROOF: Some may object to my genotypic stock definition based on Castle–Hardy–Weinberg (C–H–W) equilibrium because this equilibrium depends on the constraints of no mutation, no natural selection, no immigration and emigration occurring, and infinite population size. I regard my definition as a starting point to recognize genetic changes as they may occur in a presumed stock. The basis for these changes may then be determined and separated from true genetic differences between or among stocks. The C–H–W equilibrium can be unrealistic and anti-evolutionary because of its constraints but it does offer a means of quantifying genetic structure of a stock.

Behavioral Stock-Isolating Mechanisms in Great Lakes Fishes with Special Reference to Homing and Site Imprinting[1]

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HORRALL, R. M. 1981. Behavioral stock-isolating mechanisms in Great Lakes fishes with special reference to homing and site imprinting. Can. J. Fish. Aquat. Sci. 38: 1481 – 1496.

A moderately high degree of reproductive isolation is necessary for the formation and maintenance of discrete stocks of fish. This reproductive isolation can be developed through spawning site imprinting and homing — behavioral mechanisms that are apparently very common in fish. During some part of their early life history, the fish become imprinted to, or conditioned to, environmental characteristics of the spawning site and/or to the pheromonal characteristics of their stock. At sexual maturity, they show an orientation-homing behavior back to the natal area where spawning then occurs reinitiating the cycle. Over time, stock-specific adaptations are made to the local environment which can involve changes in the morphological, physiological, or behavioral characteristics of the fish. Research on salmonids has provided the best evidence for site imprinting and natal homing in fish. Tagging and transplantation experiments with these species have been especially important sources of information. In coho salmon (*Oncorhynchus kisutch*), olfactory homing and olfactory site imprinting have been demonstrated by artificial imprinting techniques; it was found that the critical period for imprinting occurred during smoltification at an age of 15 or 16 mo. Most species do not undergo smolting, and imprinting occurs at a very early stage in the life history. It is hypothesized that the information which is imprinted about the natal site may be obtained from one or more of the following: odors in the water flowing over the site; odors originating from the site itself; and stock-specific pheromones emitted directly from the fish or from their waste products. Differences in characteristics of homing and imprinting in relation to the formation and maintenance of stocks are discussed for several Great Lake species including coho salmon, pink salmon (*O. gorbuscha*), lake trout (*Salvelinus namaycush*), white bass (*Morone chrysops*), and walleye (*Stizostedion vitreum vitreum*). Inferences are made about how these characteristics relate to the rehabilitation of fish stocks in the Great Lakes and their tributaries.

Key words: stock-isolating mechanisms, Great Lakes fish, homing, site imprinting

HORRALL, R. M. 1981. Behavioral stock-isolating mechanisms in Great Lakes fishes with special reference to homing and site imprinting. Can. J. Fish. Aquat. Sci. 38: 1481 – 1496.

Pour que des stocks de poissons distincts se forment et se maintiennent, il faut un certain degré d'isolation reproductrice. Cette isolation peut se développer par imprégnation du site de ponte et homing — mécanismes apparemment très communs chez les poissons. À un stade quelconque du début de leur cycle biologique, les poissons deviennent imprégnés ou conditionnés par les caractéristiques ambiantes du site de ponte et (ou) aux caractéristiques phéromonales de leur stock. Quand ils atteignent la maturité sexuelle, ils ont un comportement d'orientation-homing qui les ramènent à leur lieu d'origine où ils frayent, et le cycle recommence. Avec le temps, il y a adaptation, particulière au stock, à l'environnement local, ce qui comporte des changements de caractéristiques morphologiques, physiologiques ou éthologiques. Les meilleurs preuves de l'imprégnation par le site et du retour à la rivière natale chez les poissons découlent des recherches sur les salmonidés. Des sources importantes d'information ont été des expériences de marquage et de transplantation menées avec ces

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espèces. Des techniques d'imprégnation artificielle ont démontré, chez le saumon coho (*Oncorhynchus kisutch*), le rôle de l'odorat dans le homing et l'imprégnation du site; on a découvert que la période critique pour l'imprégnation était celle de la smoltification, à l'âge de 15 ou 16 mois. La plupart des espèces n'ont pas de stade de smolt, et l'imprégnation se produit très tôt dans la vie. Nous avançons l'hypothèse que l'information ainsi imprégnée quant au lieu de naissance peut être obtenue par un ou plusieurs des moyens suivants : odeurs présentes dans l'eau coulant sur le site, odeurs prenant naissance au site même et phéromones particulières au stock émises directement par les poissons ou par leurs déchets. Nous examinons les différences de caractéristiques du homing et de l'imprégnation en relation avec la formation et le maintien des stocks de plusieurs espèces de Grands Lacs, y compris le saumon coho, le saumon rose (*O. gorbuscha*), touladi (*Salvelinus namaycush*), marigane blanche (*Morone chrysops*) et doré jaune (*Stizostedion vitreum vitreum*). Nous analysons le rôle possible de ces caractéristiques dans le rétablissement des stocks de poissons des Grands Lacs et de leurs tributaires.

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THE original fish communities which inhabited the Great Lakes included 112 species in Lake Ontario, 114 in Lake Erie, 114 in Lake Michigan, 99 in Lake Huron, and 67 in Lake Superior (Christie 1974). Within each lake many species became divided into numerous discrete or semidiscrete stocks. Ricker (1972) defines a stock[2] as "the fish spawning in a particular lake or stream (or portion of it) at a particular season, which . . . . to a substantial degree do not interbreed with any group spawning in a different place, or in the same place at a different season." Although very little is known about how much gene flow occurs between different stocks, Ricker (1972) suggests that "stock diversity and close adaptation can arise and can be maintained by selection, even when appreciable interchange of genetic material between stocks continues to occur."

Discrete or semidiscrete stocks of fish may be characterized as having different spawning locations and/or different spawning times, thereby developing some degree of reproductive isolation and by genotypic–phenotypic differences which are usually, but not always, adaptive to the local environment. Of all the species in the Great Lakes probably the greatest diversity between stocks has been described for lake trout, *Salvelinus namaycush* (Lawrie and Rahrer 1973; Brown et al. 1981; Goodier 1981). Since spawning lake trout were often commercially netted on their spawning grounds, fishermen came to know that spawning trout were found in the same places year after year, and that the timing of their spawning runs was relatively consistent from one year to the next. Trout from different spawning grounds often could be distinguished by differences in body weight, body form, skin and fin coloration, flesh coloration, and fattiness of flesh. Since lake trout with unique characteristics persisted over many years on the same spawning grounds, it is probable that these characteristics had developed, at least in part, from genetic differences arising from partial or, in some cases, almost complete reproductive isolation between breeding populations. Behavioral mechanisms used by Great Lakes fish to achieve this isolation will be described in this paper.

[2]Deme, race, and subpopulation have been used to describe population units which are similar to a stock.

Behavioral Stock-Isolating Mechanisms

Homing-orientation by sexually mature fish to the natal site and imprinting of the early life history stages at the natal site are the two most important behavioral adaptations fish use in forming and maintaining distinct stocks. Homing to the natal site for spawning has great adaptive significance. According to Leggett (1977) homing behavior: (1) maximizes reproductive success by synchronizing the return of mature animals to "proven" spawning grounds when conditions are optimum for egg and larval development; (2) regulates the number of adults utilizing a given area, thus avoiding under- or over-utilization of the habitat; and (3) facilitates reproductive isolation and therefore the development of stock-specific adaptations to each particular habitat and life history strategy. One example of a type of stock-specific adaptation is given by Brannon (1972), who found that sockeye salmon (*Oncorhynchus nerka*) fry that were hatched in inlet and outlet streams of lakes exhibited either of two responses to water currents. Fry hatched in outlet streams exhibited positive rheotaxis, which took the fry upstream into the nursery lake. Fry in tributary streams exhibited the opposite behavior, which brought them downstream into the nursery lake. These responses were shown to be under genetic control and the migrations were appropriate for finding the nursery lake of each group. Groot (1965) also found stock-specific adaptations in directional tendencies of migrating sockeye salmon smolts through a large lake toward the outlet stream.

Two phases in the homing migration of fish are usually encountered: the far-migration or open-water phase, where the return migration starts and continues toward the home-spawning grounds, and the near-home migration phase (Hasler 1966; Harden-Jones 1968).

The guidance mechanisms which are used by fish during their open-water homing movements are poorly understood (Hasler 1966; Harden-Jones 1968; Leggett 1977). Several possible orienting cues and methods that might be utilized by fish in conducting open-water migrations (far-migrations) have been discussed by Leggett (1977). They include sun orientation, polarized light, geomagnetic and geoelectric fields, temperature, water currents, ocean fronts, internal

guidance, random walks, and maximization of comfort which is "a continuous optimization of physiological and neurological states in response to a multiplicity of environmental stimuli" (Leggett 1977). Fish probably use multiple cues and several sensory systems to guide them during their long migrations. Use of multiple cues is known, for example, in other vertebrates such as homing pigeons, which can use the sun, stars, magnetic fields, odors, and low frequency sounds for determining direction and possibly geographic (map) information (Schmidt-Koenig and Keeton 1978). After carefully examining the available information on ocean migrations of the Pacific salmon, Neave (1964) suggests that "It is difficult to avoid the conclusion that throughout the period of ocean life some awareness of position in relation to the place of origin is maintained." Larkin (1975) has suggested that there would be advantages if salmon formed stock-specific schools, since it would permit greater navigational accuracy during ocean migrations (Larkin and Walton 1969).

Near-home migration, in contrast to far-migration, involves the use of cues which originate from the natal area and may be used to distinguish that area from others. The evidence suggests that these cues are primarily olfactorily-sensed substances in the water (Brett and Groot 1963; Hasler 1966; Hasler et al. 1978) although other cues and sensory systems may also be used by homing fish. Olfactory systems in fish are highly developed and extremely sensitive. Young eels, for example, can detect phenethyl alcohol at a concentration of 2.9×10^{-12} mg/L (Teichmann 1959), a truly remarkable feat. Most fish, for example, chinook salmon (*O. tshawytscha*) and coho salmon (*O. kisutch*) (Oshima et al. 1969; Dizon et al. 1973b), can recognize conspecifics by olfaction. Some fish can also olfactorily differentiate individuals of their own species (Göz 1941; Todd et al. 1967). Johnsen (1978) hypothesized that when a biologically meaningful odor is detected in a water current, it acts as a sign stimulus for initiating positive rheotaxis. Swimming upstream, in and out of the odor plume, will take the fish toward the odor source.

For an odor to be biologically meaningful in terms of homing-orientation behavior implies that the odor was imprinted on the fish at the natal site (or smolting site) during its early life history. Thorpe (1963) suggested that the traditional meaning of imprinting (e.g. Hess 1973) be extended "to cover the possibility of attachment not to a fellow member of the species but to the type of immediate environment first perceived by a newly emerged organism so that this becomes the future breeding quarters of the individual." Imprinting appears to be an ideal method for young fish to learn the characteristics of the natal area: (1) It is confined to a definite and brief period of the individual life history (the critical period); (2) once accomplished it is stable, perhaps even irreversible; (3) it may be completed long before the various specific reactions to which the imprinting pattern will ultimately become linked (i.e. homing) are established (Thorpe 1963). Information on environmental factors other than odors that might be imprinted at the natal site include magnetic fields or other geographic factors, acoustic signals, and information on the depth (pressure) of the area.

Several hypotheses concern the origin of the odors imprinted on the natal site. Hasler (1966) states ". . . each home stream acquires from the soils and plant communities of its drainage basin and in its bed, a unique organic quality which salmon learn in the early weeks of life . . . ." Wright (1964) suggested that a stream's fauna, which remains relatively stable, might be another odor source. Pheromones which could be stock-specific also have been proposed as possible odor cues which guide homing fish back to their natal grounds (Nordeng 1971, 1977; Solomon 1973; Døving et al. 1974; Larkin 1975; Døving et al. 1980; Selset 1980; Selset and Døving 1980). This hypothesis has been applied to the migrations of the Atlantic salmon (*Salmo salar*), Arctic char (*Salvelinus alpinus*), and brown trout (*Salmo trutta*). Døving et al. (1974) suggested that the char is capable of detecting and discriminating among char odors and that migratory populations of char have the ability to orient along odor tracks released from young relatives in the nursery areas of their parent river system.

Nordeng (1977) speculated that smolts migrating down river and in the ocean would leave pheromone trails and that "homeward navigation is an inherited response to population-specific pheromone trails released from descending smolt." The use of "inherited response" implies a genetic mechanism of pheromone recognition and it is not known if Nordeng still rules out imprinting to stock-specific pheromones in his hypothesis. Selset and Døving (1980) in discussing their work on pheromones in migratory char stated: "Our results, however, do not exclude an olfactory 'imprinting,' but make it likely that the possible 'imprinting' would be to substances emanating from the fishes themselves and not from vegetation or minerals (Hasler 1966)." It was suggested that bile compounds in fecal material might be the active pheromonal substance since they were detected in very low concentrations by the fish. "The odorant potency of the bile acids, their evolutionary history and variability, together with their renowned adherent properties make them interesting candidates for specific signals in the aquatic environment" (Døving et al. 1980).

Larkin (1975) discusses the use of pheromones as orientation cues and goes even further and suggests that residual pheromonal odors left from previous habitations by stock members (in pink salmon, *O. gorbuscha*, and chum salmon, *O. keta*, and sockeye in lake tributaries) might permit natal homing when there were no young remaining in the stream during the spawning migration. Selset (1980) also suggested that pheromones could "be retained at the spawning site long enough to secure homing for the fish population even if the fishes are absent for a period of time."

For species that have stocks spawning at different depths in large lakes, it seems plausible that information on the water depth (pressure) at the natal site would be advantageous during homing migrations. This could be acquired either genetically or, more likely, from imprinted information. During the stratified period in a lake it is possible to develop stratified odor distributions, since there is only a slow mixing of the water flowing above and below the thermocline. Recently, Papi (1976) has proposed an olfactory navigation system for homing pigeons based on imprinted odors directionally carried by winds. Such an idea is intriguing and one can speculate whether a similar system could have evolved in fish with waterborne odors rather than air.

Behavioral Stock-Isolating Mechanisms in Great Lakes Fishes

Three fall-spawning species, coho salmon, pink salmon, and lake trout, and two spring-spawning species, white bass, *Morone chrysops*, and walleye, *Stizostedion vitreum vitreum*, provide examples of different types of behavioral mechanisms that can be used to develop reproductive isolation between stocks. Three of these examples are native fish and two (coho and pink salmon) are introduced in the Great Lakes.

Coho Salmon

Coho salmon obtained from West Coast stocks have been introduced into the Great Lakes in large numbers since the mid-60's. The growth and survival of hatchery-reared fish has been excellent. In Lake Michigan this species usually has a 3-yr life cycle, although some males (jacks) return after 2 years. Hatchery-reared yearlings (15 mo old) are stocked into tributaries or smolting ponds in the spring. When these fish smolt, they move out of the tributaries into the lake where they remain for about 17 mo until the fall of their 3rd year, when they return to their home stream or stocking site to spawn and die.

The homing-orientation behavior of coho and other salmon to their natal spawning sites has been shown to be highly developed (reviewed by Scheer 1939; Hasler 1966; Harden-Jones 1968; Ricker 1972). Parsons (1973) stated that "Weir catches indicated strong homing instincts for coho planted in tributaries of Lake Michigan . . . 5 to 10% of the spawning adults strayed from their parent stream." This suggests that in spite of radically different geographic and environmental conditions found in the Great Lakes the homing mechanisms have become adapted to local conditions. In other experiments, coho transplanted to a new area prior to or during the smolting period returned to the new area and not to their home stream (Donaldson and Allen 1957; Jensen and Ducan 1971; Ricker 1972).

Hasler and Wisby in 1951 presented the olfactory hypothesis for salmon homing: (1) during their early life history stages, salmon become imprinted to distinctive odors of their natal tributary, and (2) adult salmon remember and use this information as a cue to relocate the stream during the spawning migration.

In an attempt to verify the olfactory hypothesis, artificial imprinting experiments with Lake Michigan coho salmon began in 1970 and have continued until the present (Dizon 1971; Dizon et al. 1973a, b; Madison et al. 1973; Scholz et al. 1973, 1975; Cooper et al. 1976; Scholz et al. 1976; Hasler et al. 1978; Johnsen 1978; Scholz 1980). In 1973–75 a large series of experiments was conducted with coho salmon which had been artificially imprinted to synthetic odors (artificial imprintants) to determine if they would return to a stream scented with that chemical. One group of fish was exposed to morpholine (C_4H_9NO) at concentrations of 5×10^{-5} mg/L, and a second group was exposed to phenethyl alcohol ($C_8H_{10}O$) at 1×10^{-3} mg/L. The fish were exposed for 43 d during their presmolt and smolt stages and a control group was untreated. This experiment was conducted in 1973 with 5000 fish in each group and again in 1974 with 10 000 fish per group. Each of the three groups was distinctively marked with a finclip.

After exposure, all three groups were released into Lake Michigan midway between two streams, the Little Manitowoc and the East and West Twin Rivers (Fig. 1). Each stream was located 4.7 km from the release point.

During the spawning migration in the fall of 1974, and again in the fall of 1975, morpholine was metered into one test stream and phenethyl alcohol into the other. Both test streams were surveyed for finclipped salmon. In addition, 16 other locations were monitored.

Data from both years indicated that most recaptured morpholine-exposed fish were taken from the morpholine-scented stream (95.0%), and of the phenethyl alcohol-exposed fish, 92.5% were captured in the phenethyl alcohol-scented stream. In contrast to the experimental fish, only 26.7 and 19.3% of the controls were recaptured in the scented streams, with the remainder straying widely (Table 1).

These experiments demonstrated that olfactory imprinting occurs in coho salmon just prior to and during smolt transformation.[3] The imprinted olfactory information is later "recalled" during the spawning migration when it is then used as an orientation mechanism. Although the olfactory hypothesis of salmon migration has been fully demonstrated only with synthetic odors, it would seem that natural odors would provide similar cues.

Since under natural conditions there are usually coho fingerlings remaining in the home stream during the spawning migration, it is possible that stock-specific pheromones emitted by these "resident" fish could serve as the olfactory cue to the upstream migrants (e.g. Nordeng 1977). It is also possible that in the artificial imprinting experiments the synthetic odors became "linked" with the pheromonal odors of the fish during the critical period for imprinting (N. Foster, U.S. Fish and Wildlife Service, 1980, personal communication). While stock-specific pheromonal homing may occur, transplantation experiments with coho, including the hatchery-reared coho stocked in Lake Michigan, showed that these fish were able to home accurately to the stream where they were released, even though there were no coho residing in the stream at the time.

Pink Salmon

Smolting, characteristic of the life history of only a few species of salmon and trout, is a process in which the fish undergoes striking physiological and behavioral changes at a relatively mature state in life, usually when they are over a year in age. In species that smolt, all of the sensory systems are fully developed and have been for most of the fish's relatively long residence in the home stream or lake. For most

[3]Olfactory imprinting may also occur in the coho during the alevin and fry stages. In many coho stocks the fry leave the home stream shortly after emerging from the redd, but apparently few survive the high salinity of the estuaries (Otto 1971). In another smolting species, the sockeye salmon, there appear to be two major imprinting periods. These occur when the fry migrate from the natal tributaries and again when the smolts depart from the nursery lake on their seaward migration.

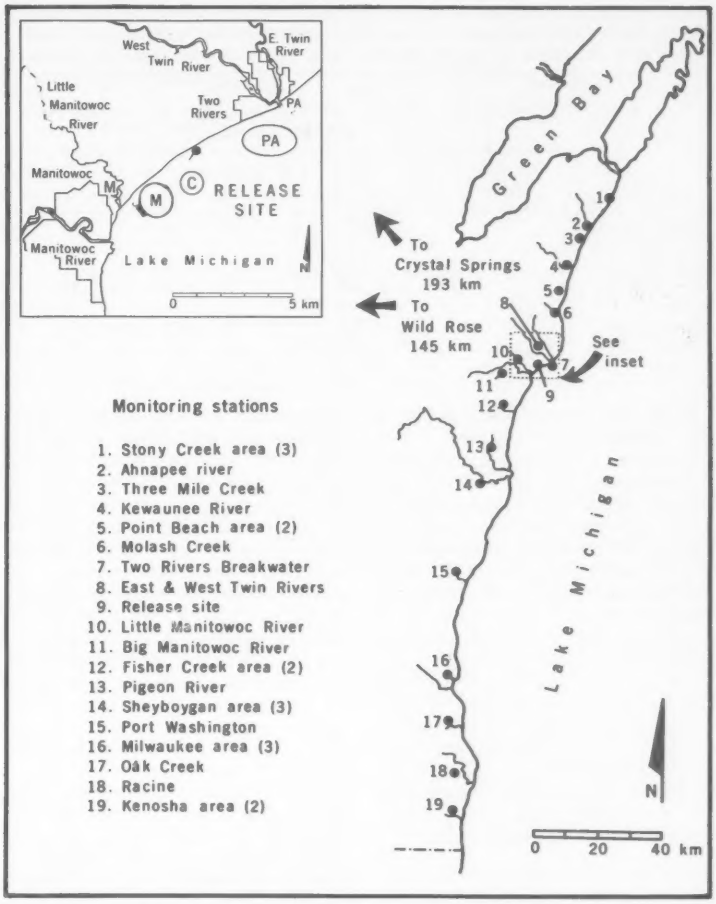


FIG. 1. The research area along the Wisconsin shore of Lake Michigan showing the locations of 19 monitoring stations where morpholine-exposed, phenethyl alcohol-exposed, and control fish were recaptured. Numbers in parentheses represent the number of streams in the general area of the monitoring station that were surveyed. Inset shows detail of the release site, the morpholine-scented Little Manitowoc River (M), and the phenethyl alcohol-scented breakwater area at Two Rivers (PA) (From Scholz et al. 1976).

other species the situation is different. A phase comparable to smolting does not occur and the fish usually leave the natal area at an early stage of development. In pink salmon, for example, the fry migrate downstream and into the estuary shortly after emerging from the gravel of the redd. If olfactory imprinting is to occur in the home stream, the olfactory system must be functional during the alevein or early fry stage. Brannon (1972) has shown that in sockeye salmon the "olfactory epithelium is well developed in the alevin and appears functional even prior to hatching." Jahn (1972) found that cutthroat trout (*Salmo clarki*) fry had structurally complete olfactory systems some 18 d before leaving the home stream. If similar olfactory development occurs in pink salmon, they would also be capable of odor detection and imprinting before leaving the home stream.

In studies of homing in pink salmon it has been shown that they tend to stray at a higher rate than other salmon. Since 21 000 pink salmon fingerlings were accidentally released into Lake Superior in 1956, they have become well established in both Lakes Superior and Huron and are now found in all of the Great Lakes (Kwain and Lawrie 1981). Presumably these salmon are gradually developing semidiscrete stocks and the opportunity for colonization will probably decrease. Although it is tempting to speculate, there is no direct evidence to indicate that either the short residence time of the fry in the home stream or the lack of young pinks in the streams

TABLE 1. Total number of morpholine-treated (M), phenethyl alcohol-treated (PA), and control (C) salmon captured at individual locations during 1974 and 1975. Data from the Little Manitowoc River (morpholine-scented) and the Two Rivers area (*p*-alcohol-scented) are printed in boldface type. Fishing effort is summarized by type and number of collecting trips at each location. From Schloz et al. 1976.

		1974						1975					
		Number recovered			Number of trips			Number recovered			Number of trips		
	Location	M	PA	C	Creel census	Gill net	Electro-fishing	M	PA	C	Creel census	Gill net	Electro-fishing
1–6.	Collection stations north of experimental area	4	3	18	457	21	28	6	1	53	303	4	14
7.	**Two Rivers Breakwater**	**3**	**118**	**15**	**184**	**3**	**1**	**3**	**192**	**12**	**126**	**14**	**1**
8.	**East and West Twin Rivers**		**15**	**7**	**123**		**9**	**3**	**8**	**21**	**17**		**14**
9.	Stocking Site	1		7	90	1				1	30		
10.	**Little Manitowoc River**	**207**	**6**	**24**	**189**		**8**	**452**	**14**	**52**	**135**		
11–19.	Collection stations south of experimental area	3	4	45	620		11		1	30	199		

at spawning time are the causes of the greater amount of straying found in pink salmon.

Bams (1976) has shown that genetic factors influence the homing behavior in pink salmon. Eggs from a transplanted stock (donor stock) of pink salmon were incubated at a hatchery in the Tsolum River system (Vancouver Island) along with hybrid eggs resulting from crossing donor females with males of the local residual stock. Some of the donor stock returned to the river, apparently through imprinting alone. The hybrid stock, however, returned to the river in large numbers although returns to the natal tributary were lower than normally occurred with the native stock. Little is known about what aspect of the homing process is disrupted, but it points out the importance of genetic adaptation for the survival of a stock. Bams pointed out that a given number of males have an immense pool of reproductive cells as compared to a similar number of females. He states that "What remains of a locally adapted gene pool could therefore be greatly expanded and preserved by utilizing the available males to fertilize large numbers of eggs imported from a donor stock."

LAKE TROUT

Although natal homing in lake trout has not been demonstrated, it is certainly suggested by the fidelity of repeat homing to specific spawning reefs (Martin and Olver 1980; Swanson and Swedberg 1980). For example, in tagging experiments on Gull Island Schoal in Lake Superior, native lake trout showed an 8.6% return and 98.6% correct homing (Swanson 1973). In a recent study of lake trout in Lake Opeongo using tagging and ultrasonic tracking methods, MacLean et al. (1981) concluded that the lake trout they were studying wandered extensively and possibly were not homing to specific shoals to spawn.

Lake trout spawn in the fall of the year on reef and shoal areas, depositing their eggs amid rock rubble. In the spring the eggs hatch and the sac fry remain hidden in the rocks for several weeks until the yolk sac is absorbed. Shortly afterwards, in the swim-up stage, the fry migrate to the surface to fill their swim bladders (Balon 1980). How frequently the swim-up fry return to their natal area is unknown, but fry originating from deep reefs would probably be displaced by water currents. Lake trout fry were captured in the vicinity of a shallow-water artificial reef in Lake Superior for almost 3 m (Peck 1981). Although it is not known what proportion of the fry remain near the reef, it does indicate that at least some fry remain near the natal area after the swim-up stage. As the fry grow into young fingerlings they begin to migrate into deeper water (Eschmeyer 1956). The critical period for olfactory imprinting in lake trout, therefore, is probably during the period from hatching through the yolk sac stage to the swim-up stage. Richard Saunders (1980, personal communication) feels that imprinting in lake trout may be associated with its first major movement or displacement from the natal area, that is the swim-up migration. Although the detailed work on the developmental anatomy of the olfactory system in lake trout has just started, preliminary histological studies suggest that the system is functional by the swim-up stage (N. Foster personal communication).

Although almost nothing is known about the mechanisms of imprinting in lake trout, there are at present two groups engaged in lake trout imprinting research. Neal Foster (personal communication; Foster and Berlin 1980) has obtained evidence of pheromone-mediated spawning site selection in laboratory studies of lake trout. Males performed species-typical substrate-rubbing behavior and subsequently spawned with ripe females on two artificial reefs with fry feces and mucus, but rarely on two other reefs without such conspecific odors. Foster's hypothesis is that stock-specific pheromones, which serve as natural imprintants emitted from remains of fry feces and mucus from the previous spring, attract or guide members from the same stock to the natal reef to spawn. Imprinting to the pheromones would occur during the trout's early life history on the reef.

The writer has artificially imprinted two groups of lake trout to phenethyl alcohol: one group during the period from the eyed-egg stage until the early fingerling stage; the other group at the yearling stage 1 mo before stocking. These fish, along with controls, were stocked into Lake Michigan for a field test using synthetic decoy odors. Each group contained about 64 000 fish and a small number of each group was retained in the laboratory for behavioral experiments. Two of the objectives of these studies are to determine critical periods for olfactory imprinting and to assess the relative importance

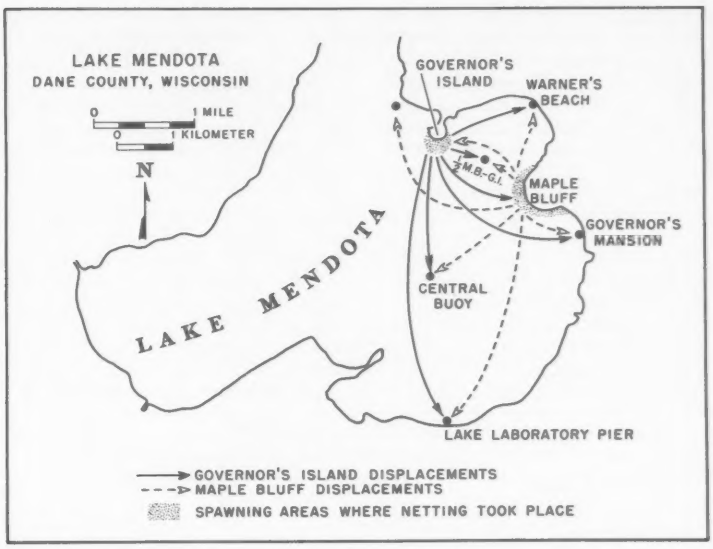


FIG. 2. Locations of white bass spawning grounds at Maple Bluff and Governor's Island, Lake Mendota, Wisconsin, and locations of the release sites used for the 1957 and 1958 white bass displacement experiments (From Horrall 1961).

of natural and synthetic odors in the decoy experiments.

WHITE BASS

Although white bass are abundant in some areas of the Great Lakes, especially in Lake Erie, there has been relatively little work done on white bass stocks. Therefore, work will be described on the reproductive behavior of two stocks of white bass in Lake Mendota, Wisconsin. There are two major white bass spawning grounds, Maple Bluff and Governor's island. Both are located on the north shore of this 39.4-km^2 lake and are separated by a distance of 1.6 km. White bass congregate on these grounds at spawning time in mid-May when water temperatures reach 13°C; the spawning run is over by mid-June when temperatures reach 26°C. These two spawning populations were studied extensively from 1955 to 1960 (Hasler et al. 1958; Horrall 1961).

To study the homing behavior of these two spawning groups, displacement experiments with tagged fish were conducted. Spawning fish were captured in fyke nets on each of the spawning grounds, tagged, and then displaced to eight different locations in the lake (Fig. 2). The results of these experiments showed that fish from each of the spawning grounds returned to their "home" grounds with great accuracy and little straying (Fig. 3). This was true even when fish from one spawning ground were taken and released directly on the other spawning ground. The results from these experiments indicated that similar homing ability was exhibited by both male and female fish, and by fish from each of the spawning sites. Of the 553 recaptures made from the 3793 fish tagged in 1957 and 1958, 89.2% returned to their correct spawning grounds.

Over the entire course of the 5-yr study 9071 releases and re-releases of tagged white bass were made. Of the 1381 recaptures, 88.8% had "homed" correctly. The evidence strongly supports the hypothesis that white bass were homing to a specific spawning ground during the course of a single spawning season. The preference for a specific spawning site was also maintained in the succeeding spawning seasons by individual fish. Of 621 fish which were recaptured 1 or 2 yr after tagging, 83.1% was recaptured on their home spawning ground.

In addition to the observed accuracy and specificity of homing, the data also indicated that a large majority of the displaced fish actually returned to their spawning ground, and that this return was rapid. Tagged fish released on their spawning ground without being displaced gave similar recapture-percentages and time-lapses between release and recapture as did those fish that were displaced.

Further information on homing and homing-orientation was obtained when 17 spawning white bass were displaced from the Maple Bluff Spawning ground to a mid-lake release site and tracked with ultrasonic transmitters during daylight hours. The movement patterns clearly indicated a directional tendency towards their home spawning ground and suggested that white bass possess some type of open-water orientation mechanism in relation to their spawning ground during the spawning season (Hasler et al. 1969).

The studies on white bass in Lake Mendota showed that there was a homing-orientation back to a specific spawning site during one spawning season, and to the same site in subsequent years. At least three possible conditions can be suggested to explain this behavior. (1) A limited, discrete range of dispersal of the young and adults could occur around

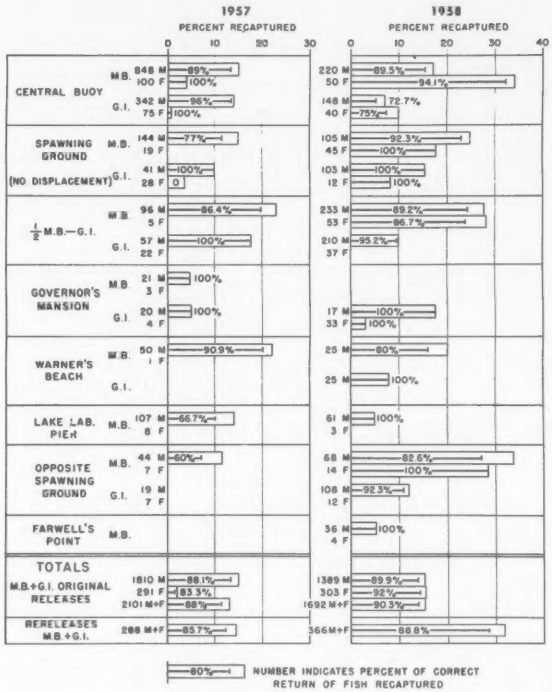

1957
PERCENT RECAPTURED
0 10 20 30
1958
PERCENT RECAPTURED
0 10 20 30 40
CENTRAL BUOY
M.B. 848 M 89% 100 F 100%
G.I. 342 M 96% 75 F 100%
220 M 89.5% 50 F 94.1%
148 M 72.7% 40 F 75%
SPAWNING GROUND (NO DISPLACEMENT)
M.B. 144 M 77% 19 F
G.I. 41 M 100% 28 F 0
105 M 92.3% 45 F 100%
103 M 100% 12 F 100%
½ M.B.—G.I.
M.B. 96 M 86.4% 5 F
G.I. 57 M 100% 22 F
233 M 89.2% 53 F 86.7%
210 M 95.2% 37 F
GOVERNOR'S MANSION
M.B. 21 M 100% 3 F
G.I. 20 M 100% 4 F
17 M 100% 33 F 100%
WARNER'S BEACH
M.B. 50 M 90.9% 1 F
G.I.
25 M 80%
25 M 100%
LAKE LAB. PIER
M.B. 107 M 66.7% 8 F
61 M 100% 3 F
OPPOSITE SPAWNING GROUND
M.B. 44 M 60% 7 F
G.I. 19 M 7 F
68 M 82.6% 14 F 100%
108 M 92.3% 12 F
FARWELL'S POINT
M.B.
36 M 100% 4 F
TOTALS
M.B.+G.I. ORIGINAL RELEASES
1810 M 88.1% 291 F 83.3% 2101 M+F 88%
1389 M 89.9% 303 F 92% 1692 M+F 90.3%
RERELEASES M.B.+G.I.
288 M+F 85.7%
366 M+F 88.8%
80% NUMBER INDICATES PERCENT OF CORRECT RETURN OF FISH RECAPTURED

FIG. 3. Results of displacement experiments of white bass from Maple Bluff and Governor's Island spawning grounds, 1957 and 1958 (From Horrall 1961).

the natal spawning area. Homing would occur because the natal spawning site was the only one available within the "home" range. (2) Repeat homing occurs to the site where the fish first spawned. Any return to the natal spawning site would be purely accidental but could occur frequently because of the limited number of spawning sites within the lake. (3) Homing occurs to the natal site at the first and subsequent spawnings. Although almost nothing is known about the distribution of young white bass, the nonspawning season distribution of 162 tagged adults recaptured by anglers indicated that Maple Bluff and Governor's Island fish were distributed over the entire lake with no tendency to remain near the spawning grounds. This implies a more sophisticated homing mechanism than would be involved in a situation of limited range and subsequent utilization of a spawning site in the immediate area. Although repeat homing to the site of first spawning can explain the observed homing behavior, two lines of evidence suggest that natal homing was involved, and that there were two semidiscrete stocks of white bass in Lake Mendota. There were small but consistent differences between the age compositions found at the two spawning grounds during the study period, suggesting that differential site-specific recruitment had occurred and that it was maintained by homing (Zijlstra 1958). Wright and Hasler (1967) found that there were differences in the blood serum proteins between the Maple Bluff and Governor's Island spawning groups which also suggested that natal homing was occurring. How, then, do sexually mature white bass locate their natal spawning site?

In one experiment designed to test if olfaction is used by homing white bass, 322 fish had their olfactory sacs occluded. They were then displaced 2.4 km from their home spawning ground to a mid-lake site and released with 328 control fish. Twenty-one percent of the control fish were recaptured, of which 92.8% were at the home site. In contrast, only 6.8% of the olfactory-occluded fish were recaptured and less than half (45.5%) were at the home site. Although other interpretations of these results are possible, such as the anosmia reducing the sex drive, olfaction does seem to play a role in the homing process in white bass.

As discussed previously, at least two kinds of olfactory information may be imprinted on larval white bass while they are still on the spawning grounds after hatching: (1) The characteristic odors of the water on the spawning ground (other than pheromones of white bass on the grounds). (2) Pheromones emitted from adult and/or young white bass on the grounds, which are assumed to be stock-specific pheromones.

The critical period for olfactory imprinting in white bass is hypothesized to be from shortly after hatching until the swim-

up larvae are displaced from the spawning ground. This may be as soon as 4 or 5 d after hatching. Since white bass eggs hatch relatively quickly (~ 4.5 d at 14°C, 2 d at 20°C; and 1 d at 26°C [Wright 1964; McCormick 1978]), larvae must be abundant on the ground while spawning activity is still in process. In addition, since white bass is a strongly schooling species, any further association with other individuals from the same grounds, perhaps in a nursery area, could reinforce the stock-specific pheromonal imprint if this occurred before the end of the critical period. In fact there is good evidence that schooling behavior is at least in part mediated by pheromones, and therefore it is entirely possible that individuals from specific stocks may form their own schools.

If there were imprinting to white bass pheromones, and not to the other odors in the water, during the larval stages, then how could a pheromone mechanism serve in locating the natal ground during the spawning migration of a recruit spawner? It could be residual pheromonal odors remaining on the spawning ground as has been suggested for lake trout. However, it has been observed in many spawning groups of fish that the largest and oldest members will arrive first on the spawning grounds (Table 2). This phenomenon was found to be developed strongly in white bass. There was a progressive decrease in the mean length and age of both male and female spawners during the spawning period (Fig. 4 and 5). These changes were regular and followed similar patterns on both spawning grounds. Although this process is most likely a function of age-specific differences in the seasonal maturation cycle, it might, nevertheless, serve as stock-specific pheromonal cues emitted from the earlier arriving repeat spawners (fish 4 yr and older) to guide the recruit spawners (fish 2 and 3 yr old) to their natal grounds for the first time. Undoubtedly there would be the opportunity of learning additional cues regarding the spawning ground's location and characteristics during the first and subsequent spawnings.

In spite of the large amount of work done on this species,

TABLE 2. List of species known to arrive on the spawning grounds at different times, depending on size or age.

Family and species	Reference
I. Species in which the older or larger fish arrive first on the spawning ground	
Spring spawning fish	
Clupeidae:	
Atlantic herring, *Clupea harengus harengus*	Lea 1929 Popiel 1958
Salmonidae:	
Cutthroat trout, *Salmo clarki*	Cope 1957
Catostomidae:	
Dwarf sucker, *Catostomus commersoni utawana*	Dence 1948
Gadidae:	
Skrei (cod), *Gadus callarias*	Rollesfsen 1956
Hake, *Merluccius merluccius*	Hickling 1934 (from Graham 1956)
Whiting, *Gadus merlangus*	Bowers 1954
Percichthyidae:	
White bass, *Morone chrysops*	Horrall 1961
Percidae:	
Darter sp. (e.g. *Etheostoma* sp.)	Winn 1958
Yellow perch, *Perca flavescens*	el-Zarka 1959
Walleye, *Stizostedion vitreum vitreum*	Bodaly 1980
Scombridae:	
Atlantic mackerel, *Scomber scombrus*	Sette 1950
Summer spawning fish	
Salmonidae:	
Artic char, *Salvelinus alpinus*	Selset and Døving 1980
Fall spawning fish	
Salmonidae:	
Lake herring, *Coregonus artedii*	Smith 1956
Brown trout, *Salmo trutta*	Stuart 1953
II. Species in which the younger or smaller fish arrive on the spawning ground first	
Fall spawning fish	
Clupeidae:	
Atlantic herring, *Clupea harengus harengus*	Hodgson 1957
Salmonidae:	
Lake trout, *Salvelinus namaycush*	Martin 1956
Cottidae:	
Longhorn sculpin, *Myoxocephalus octodecemspinosus*	Morrow 1951

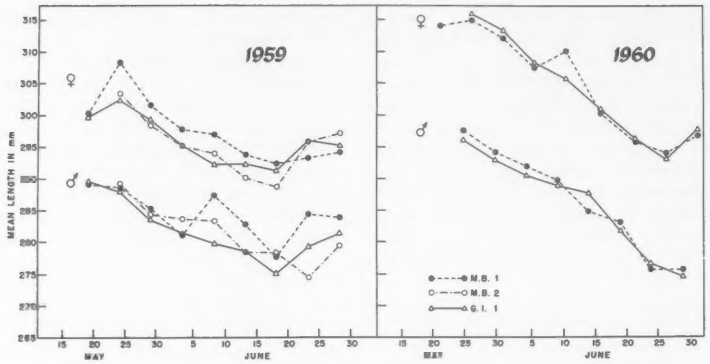


FIG. 4. Mean lengths of samples of male and female white bass, by 5-d sampling periods, on Maple Bluff and Governor's Island spawning grounds, Lake Mendota, 1959 and 1960. M.B.1 and M.B.2 represent different nets at Maple Bluff; G.I.1 is the netting station at Governor's Island (from Horrall 1961).

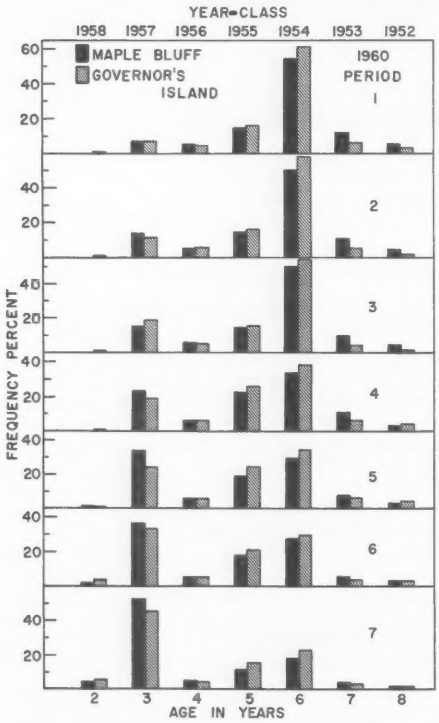


FIG. 5. Age-frequencies for each of the seven periods, Maple Bluff and Governor's Island spawning grounds, Lake Mendota, 1960. Male fish only. Period 1: May 23–27; period 2: May 28–June 1; period 3: June 2–6; period 4: June 7–11; period 5: June 12–16; period 6: June 17–21; period 7: June 22–26 (From Horrall 1961).

there is no evidence indicating whether young white bass on their natal grounds imprint to odors, or if they do whether the natural imprintants originate from the spawning ground and associated water masses or from stock-specific pheromones originating from the fish themselves or from both.

WALLEYE

Walleyes spawn in both lakes and rivers and often have long-range spawning migrations. Repeat homing to specific spawning grounds is well documented (Olson et al. 1978). There is no direct evidence that homing is back to the natal area, but it is widely accepted that it is (Regier et al. 1969; Loftus 1976; Spangler et al. 1977; Colby and Nepszy 1981).

Recently Olson et al. (1978) presented a hypothesis that "walleye homing is an adult-learned behavior rather than a natal-imprinted response." Their major argument centers around the transport of eggs and fry away from the natal area and, presumably beyond where imprinting could occur. It is unknown what proportion of the eggs drift away, but certainly the larval stages remain on the spawning grounds for only a short period of time. If olfactory imprinting can occur on the spawning grounds then the olfactory system must be developed enough to be functional during the larval stage shortly after hatching. This information is not available. If swim-up larvae form schools or aggregations that remain together, then there is the possibility that imprinting to stock-specific pheromones by members of the group could occur as they are being transported away from the spawning grounds. As with white bass, residual pheromonal odors remaining on the spawning grounds and/or odors from the larger, older walleyes arriving earliest on the spawning grounds (Bodaly 1980) might produce odor trails for guiding recruit spawners to their natal grounds. Further research is needed to tell us the degree of use of imprinted vs. adult-learned behavior in the homing of walleyes.

Discussion

It has long been known that salmonids are able to home to

their natal grounds with remarkable precision even though they conduct migrations of great length and complexity. To evolve and maintain these highly specialized reproductive and behavioral adaptations, there must be a high degree of reproductive isolation (Leggett 1977). Any increase in the precision of homing and therefore of reproductive isolation can result in the development of adaptations allowing more complex life history strategies. This is well illustrated in sockeye salmon, a species exhibiting precise homing (Hartman and Raleigh 1964), where investigators have demonstrated stock-specific differences in both rheotactic responses in fry (Brannon 1972) and in direction of migration in smolts in a large, complex lake system (Groot 1965). Barns (1976) has shown that local genetic adaptation of a stock increases the homing ability in pink salmon, a species with higher straying rates than the sockeye. Although specific genetic programs are important in adapting to local environments, an open-genetic program, such as the capacity for imprinting (learning) information about the natal area, has the effect of "enriching the behavioral program [that] has the great advantage of being able to store far more complex objects of behavior than the genetic program" (Mayr 1974).

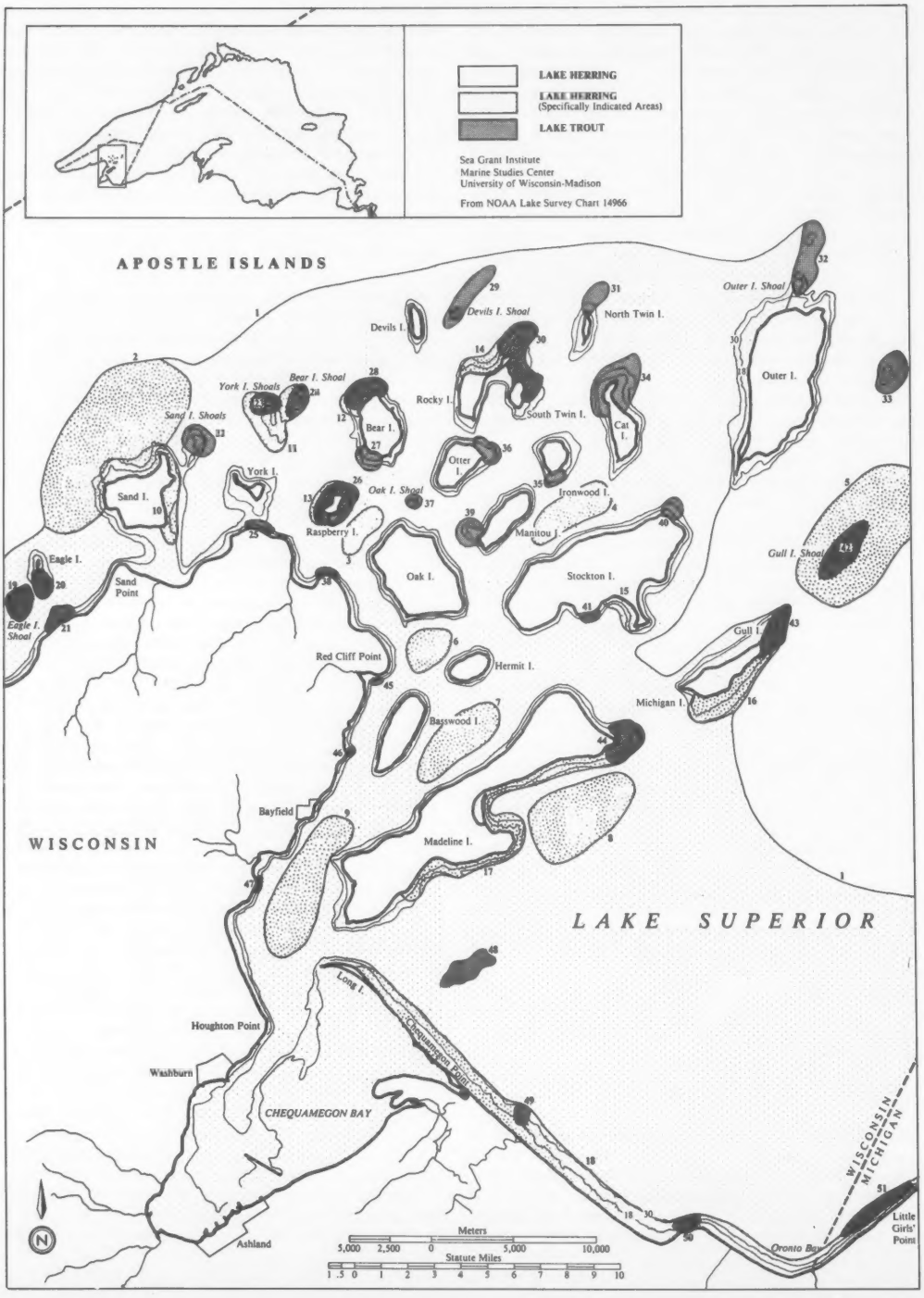
Less precise homing ability and the associated decreased reproductive isolation between stocks may commonly occur in many species of non-salmonid fishes. Genetic information concerning migration routes, location of the natal site, or specialized directional behavior in the early life history stages is probably not found in most species, so that imprinted information becomes the major, if not only, link with the natal area. Although the specific types of information imprinted are not known as yet for any species, it is possible that pheromonal mechanisms are more important in natal homing and stock formation than was formerly believed (Teeter 1980). Since vertebrate pheromones are usually complex mixtures of compounds, small variations in biochemical structure and proportions of component compounds can change the odor qualities of the pheromone (Wilson 1970; Stoddart 1980). Such changes might be incorporated rather quickly into the genetic makeup of a developing stock. If the pheromonal scent blend of a stock were imprinted at an early age, its subsequent use by a young spawner in locating its natal grounds could be through odor trails emitted by older spawners already occupying the grounds; by odor trails from pheromonally "scent-marked" grounds, for example with body mucus and fecal material (Foster and Berlin 1980); or by odor trails (plumes) from both sources. The materials which would "mark" such a spawning ground might build up over time, being renewed continuously at each spawning and hatching time (depending on the pheromonal strategy of the species), to form a traditional stock-specific spawning site abundantly supplied with pheromones for imprinting young and for attracting spawners.

Previous studies on the behavioral mechanisms of natal spawning site selection have been preoccupied with homing. However, straying is obviously important for colonization, recolonization, and for maintaining genetic variability in the stocks. Aside from nature's continuing experiments, man has attempted many transplantations of fish stocks. Most of these transplants have failed, not in the sense that there were no fish returning to the new site, but rather in the long-term failure to form self-sustaining stocks at the new location (Blackett 1979; Helle 1981). There are many reasons for the failures which occur in stock transplants, but these failures are probably most strongly linked with (1) stocking in locations with unsuitable spawning sites or nursery areas; (2) stocking from genetically inappropriate donor stocks; (3) stocking during a non-imprintable period in the species life history or stocking during an imprintable period but at an inappropriate location; and (4) stocking without taking into consideration the possibility that pheromones may be utilized for homing, and that none are available at the stocking location unless they are specially provided.

Stocking Locations

Calaprice (1969) has suggested that in salmonids "we might well expect a distribution of semi-isolated locally adapted populations undergoing continuous change." The spatial distribution of these local populations, or stocks, depends largely on where suitable spawning substrate and favorable conditions for the young are found together. Recently there has been a dramatic increase in our knowledge of where fish spawned historically and where fish are now spawning. On the Canadian side of Lake Huron, Smith (1968) charted the locations of over 150 lake trout spawning grounds from information obtained through interviews with commercial fishermen. These once abundant and productive lake trout stocks are now all extinct except for two small residual stocks in Parry Sound and McGregor Bay. In the Apostle Islands of Lake Superior, Coberly and Horrall (1980) charted 33 former lake trout spawning grounds and 17 lake herring (*Coregonus artedii*) spawning grounds, again from information from commercial fishermen (Fig. 6). Gull Island Shoal, Cat Island Shoal, and Sand Cut Shoal are the only spawning grounds in the Apostle Islands where the native lean lake trout have survived. However, only the Gull Island Shoal stock has made a significant recovery since initiation of sea lamprey control (Swanson and Swedberg 1980). Lake herring stocks in the Apostle Islands are much reduced and some may have been lost (Selgeby 1979). These are just a few examples of what has happened to many other Great Lakes species — unoccupied spawning grounds where there were once traditional, productive ones. In attempts to rehabilitate these lost stocks it would be advisable to concentrate stocking efforts on the historically most productive traditional spawning grounds in each area. Spawning grounds do not usually have continuously good spawning substrate, and the best substrate is often found widely scattered throughout the area (Stamm et al. 1981; Brown et al. 1981). If this is the case, specific stocking practices may be needed, such as eggs or sac fry being seeded by divers directly on what appears to be the best substrates found on the grounds. For example, surveys to determine the locations of suitable spawning substrates for lake trout have been made by divers swimming transects over reefs (Stamm et al. 1979, 1980, 1981). Twenty-four reefs and shoals which were traditional lake trout spawning grounds have been surveyed in Lakes Michigan and Superior.

Originally many species which formed lake-spawning stocks also formed river-spawning stocks. These river-spawning stocks may have made strong contributions to the early productivity of the lakes (Smith 1972). These included lake trout, lake whitefish (*Coregonus clupeaformis*), lake her-


LAKE HERRING
LAKE HERRING
(Specifically Indicated Areas)
LAKE TROUT
Sea Grant Institute
Marine Studies Center
University of Wisconsin-Madison
From NOAA Lake Survey Chart 14966
APOSTLE ISLANDS
Devils I.
Devils I. Shoal
North Twin I.
Outer I. Shoal
Outer I.
York I. Shoals
Bear I. Shoal
Rocky I.
South Twin I.
Cat I.
Sand I. Shoals
Bear I.
Otter I.
York I.
Sand I.
Oak I. Shoal
Ironwood I.
Raspberry I.
Manitou I.
Gull I. Shoal
Eagle I.
Sand Point
Oak I.
Stockton I.
Eagle I. Shoal
Gull I.
Red Cliff Point
Hermit I.
Michigan I.
Basswood I.
Bayfield
WISCONSIN
Madeline I.
LAKE SUPERIOR
Long I.
Houghton Point
Washburn
Chequamegon Point
CHEQUAMEGON BAY
WISCONSIN
MICHIGAN
Little Girls' Point
Oronto Bay
Ashland
N
Meters
5,000 2,500 0 5,000 10,000
Statute Miles
1 5 0 1 2 3 4 5 6 7 8 9 10

ring, walleyes, yellow perch (*Perca flavescens*) and probably lake sturgeon (*Acipenser fulvescens*), northern pike (*Esox lucius*), and burbot (*Lota lota*). If pollution and silting can be reduced from some of the tributaries to the Great Lakes, then it might become possible to reestablish some of the species which formally had river-spawning stocks. Monitoring the recovery of river stocks may be somewhat easier than that of lake stocks.

Donor Stocks

Where remnant stocks of a species remain, they should be protected and encouraged as they offer probably the most rapid means of rehabilitation. Where remnant stocks do not exist, or similar stocks are not available, then rehabilitation may best be carried out by introducing offspring from a wide variety of available stocks and/or offspring of all possible crosses between a variety of stocks (Krueger et al. 1981). This would ensure a broad genetic variability (heteozygosity) for natural selection to act upon so that the best traits associated with adaptation and survival can be rapidly incorporated into the new stock's genetic makeup (Ihssen 1976; Krueger et al. 1981).

Imprinting

If stocked fish are to return to a specific area to spawn, then the appropriate information must be available to them during the critical period for imprinting. This is equally true for acquiring odor information from the natal stocking site and from pheromonal information. However, the timing of the critical period for olfactory imprinting is known for only a few species of fish. In coho salmon imprinting has been shown to occur during smoltification, and this is probably true for other salmon and trout which smolt, although an earlier critical period for imprinting may also occur during the fry stage. Because of the lack of experimental data, the critical period for imprinting in most other species can be inferred only from life history information. Although olfactory imprinting is usually considered as being possible only during life history stages with functionally developed olfactory systems, it is possible that imprinting could occur at earlier stages in some species, for example, in the egg stage. Research designed to determine when developing eggs and fry are susceptible to imprinting is needed, especially in species where eggs or fry are rapidly displaced from the natal area.

Pheromonal Homing

If the imprinted information concerning the natal site is obtained from odors in the water flowing to and over the site, then newly stocked fish, assuming they are imprintable, will have all the appropriate information they need for imprinting and for future homing. However, if there is a pheromonal mechanism for homing, then the appropriate pheromonal information may not be available either to the newly stocked fish or to the fish when they subsequently returned to spawn. In the pheromonal homing of lake trout, as suggested by Foster and Berlin (1980), the sac fry hatched from eggs planted on a barren reef might become imprinted to odors from their own egg membranes, mucus, and feces, but these materials and their odors would probably be lost in the 5 or 6 years before the fish matured and returned to spawn. In this case the pheromonal link with the past had been broken, in natural stocks pheromonal materials would be renewed yearly and "stockpiled." To restart this cycle it may be necessary, for example, to collect waste materials from a lake trout hatchery and place them on the stocked reef during the fall when the trout will be spawning for the first time (B. Swanson, 1980, personal communication), or to place caged lake trout spawners from the donor stock on the reef during the same period. Artificial olfactory imprinting may also be an approach to restarting the cycle, decoying the fish back to the reef for their first spawning.

In conclusion, our knowledge is meager on most aspects of behavioral stock-isolating mechanisms in fishes. For example, only recently has homing been verified in such common Great Lakes species as lake whitefish (F. Copes, 1981, personal communication) and white sucker (*Catostomus commersoni*) (M. Imhof and R. Horrall, 1980, personal communication). Research directed toward understanding natal site imprinting and possible pheromone imprinting mechanisms and associated homing pheromena in fishes should be encouraged as they may become key elements in the successful rehabilitation of stocks.

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Fig. 6. Locations of the historical spawning grounds of lake trout and lake herring in the Apostle Islands, Lake Superior (from Coberly and Horrall 1980). Lake trout spawning grounds mentioned in the text are Gull Island Shoal (number 42), Cat Island Shoal (number 34), and Sand Cut Shoal (number 48).

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Stocks are Chameleons: Plasticity in Gill Rakers of Coregonid Fishes[1]

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The characters that apparently render a stock of fish distinctive may in reality be a reflection of the presence or absence of other fish species with which the stock shares its environment. Over the northern hemisphere, the whitefish genera *Coregonus*, "*Leucichthys*," and *Prosopium* offer striking examples of morphological characters being displaced because of coinhabiting species. Whenever one of the groups is missing, another tends to shift its gill rakers so as to fill in the vacant part of the spectrum in gill-raker counts. Plankton-feeding lake whitefish (*Coregonus clupeaformis*) having many long gill rakers exist in several lakes sympatrically with bottom-feeding lake whitefish having fewer and shorter gill rakers, but only if the even more specialized plankton-feeding species of ciscoes are absent. Lake whitefish in Yukon Territory have on the average fewer rakers in those lakes that contain ciscoes than in those that do not. Artificial transplants demonstrate that gill-raker characteristics can change quickly in a new environment. Gill-raker count is less subject to phenotypically induced variation from environmental influences than are most morphological characters, but it is not immune. Partial hybridization, where bimodal populations are maintained by a balance between gene flow and selection, also poses special problems for the stock concept. When employing even relatively stable characters such as gill-raker counts, one should beware that the "stocks" may be chameleons which shift their appearance in response to the biological color of their surroundings.

Key words: coregonids, whitefish, gill rakers, phenotypic variation, hybridization, selection, transplants, stocks

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Il est possible que les caractères qui font qu'un stock de poissons se distingue d'un autre reflètent en réalité la présence ou l'absence d'autres espèces de poissons avec lesquelles le stock partage son environnement. Dans l'hémisphère nord, les genres *Coregonus*, «*Leucichthys*» et *Prosopium* offrent des exemples frappants de caractères morphologiques que la cohabitation avec d'autres espèces a modifiés. Quand un de ces groupes est absent, un autre tend à modifier ses branchicténies de façon à occuper la portion vacante du spectre de comptages de branchicténies. Des grands corégones planctivores à longues branchicténies vivent sympatriquement avec des sujets de la même espèce qui se nourrissent au fond et qui possèdent des branchicténies moins nombreuses et plus courtes, mais seulement quand les espèces de ciscos, planctivores encore plus spécialisés, sont absents. Les grands corégones du Territoire du Yukon ont en moyenne moins de branchicténies dans les lacs qui contiennent des ciscos que dans ceux où ces derniers sont absents. Des peuplements artificiels démontrent que les caractéristiques des branchicténies peuvent changer rapidement dans un environnement nouveau. Le nombre de branchicténies est moins sujet à une variation provoquée phénotypiquement par des influences ambiantes que la plupart des caractères morphologiques, mais il n'en est pas pour cela indépendant. L'hybridation partielle, qui fait que des populations bimodales se maintiennent grâce à un équilibre entre le flux génique et la sélection, obscurcit également la notion de stock. Quand on fait appel même à des caractères relativement stables, tels que les branchicténies, on doit être sur ses gardes : les «stocks», tout comme les caméléons, peuvent modifier leur apparence en réponse à la «coloration biologique» de leur environnement.

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STOCKS, subspecies, species, and even genera of coregonid fishes have been identified principally by the number of gill rakers. No other character has been found in whitefishes which is so reliable and which has so high a hereditary component (Svärdson 1952). Yet despite its indispensable role in taxonomic identification, gill-raker number in coregonids can display striking adaptive radiation (when other species are absent) or character displacement (when they are present). Gill-raker count of each species seems to interdigitate with the counts of other cohabiting species, so as to follow a sort of Parkinson's principle: "gill raker counts expand to fill the available niches."

The phenomenon of gill-raker plasticity will be illustrated at all levels, from long-standing sharply delineated sympatric genera and species, through sibling pairs which originated more recently (in geological terms), to diverging races within single water bodies a few thousand years old, and finally to shifts due to human intervention within a century or even a decade. Such a spectrum of gill-raker adjustments shows that even this most reliable of characters cannot safely be used to equate two allopatric stocks because they appear similar, nor to identify, through time, stocks in a changing environment. In gill-raker counts (and even more so in most other characters which are subject to additional environmental modifications), "stocks" are chameleons which shift their appearance in response to the biological color of their surroundings.

Plasticity of Same Genus in Different Lakes

Striking examples of character convergence can be found between the genera and subgenera of whitefishes. In each major geographic region the coregonid species present tend to cover the whole range of potential gill-raker counts. If a genus or subgenus that typically fills one segment of the range is absent, then, provided there has been sufficient time, species from another genus or subgenus will be found to fill the gap. Where time has been insufficient there may be unoccupied segments of the gill-raker array, but then the species present often give the impression, through skewness or increased variability, of being in the process of moving towards occupying the gap. Although gill-raker number is the character stressed here, a whole suite of associated characters all related to trophic status often shifts along with gill-raker number. Thus, open-water plankton feeders with high gill-raker counts often also have long rakers, large terminal mouths, large eyes, compressed bodies, and silvery coloration. This convergent suite of planktivore characters probably has evolved at least three times, to the discomfiture of taxonomists.

Three full genera are currently recognized among the whitefishes (which form the family Coregonidae according to some authors, or the subfamily Coregoninae within the family Salmonidae according to others). One of these, *Stenodus*, is a highly distinctive piscivore which is excluded from further discussion here (and which does not occur in any of the lakes in Fig. 1). The other genera are *Prosopium* and *Coregonus*. The genus *Coregonus* is in turn divided into the subgenus *Leucichthys* (the "ciscoes," highly adapted for plankton feeding) and the subgenus *Coregonus* (whitefishes, usually adapted for more catholic or benthic feeding). For convenience, only the subgeneric names *Coregonus* and *Leucichthys* will be used hereafter, adopting the convention that these are short forms for *Coregonus* (*Coregonus*) and *Coregonus* (*Leucichthys*), respectively. On average, species of *Prosopium* have low gill-raker counts, *Coregonus* have medium counts, and *Leucichthys* have high counts, but there can be some overlap. *Prosopium* is most diverse in North America, *Coregonus* in Eurasia, and *Leucichthys* in the Great Lakes region of North America (Smith 1957).

Each of the three groups has distinctive characters in addition to gill-raker number. The full genera *Prosopium* and *Coregonus* are almost certainly each monophyletic, the former being distinguishable by a basibranchial plate and other osteological features, parr marks in the young, a single nostril flap (Norden 1961, 1970), and probably distinctive biochemistry. The subgenera *Coregonus* (*Leucichthys*) and *Coregonus* (*Coregonus*) are probably (but not certainly) each monophyletic, the latter being distinguishable by a characteristically shaped maxilla and supramaxilla and mesethmoid, a projecting or terminal lower jaw, a maxilla usually reaching behind the front eye margin, and perhaps distinctive biochemistry (Shaposhnikova 1970; Behnke 1972; Reshetnikov 1977).

Figure 1 shows gill-raker counts of coregonid species in representative lakes. Lake Superior, in the center, has at least seven sympatric coregonid species, including all three taxonomic groups. The relationships of raker counts among these species groups is repeated in broad pattern although not in detail in hundreds of North American lakes. On either side are shown counts in other lakes where one or two of the groups are lacking; in these, the range of counts can be seen to be at least partially filled by a remaining group. Following is a consideration of each group in turn and how it has responded to the presence or absence of the other groups.

The lake whitefishes, *Coregonus clupeaformis* are least speciose in North America where plankton feeding niches are usually filled by *Leucichthys*. One distinctive subarctic species, the broad whitefish *C.* (*Coregonus*) *nasus*, has few short gill rakers and a bottom-feeding habit; it does not occur in any of the lakes in Fig. 1 and will not be discussed further. The widespread North American form is the humpback whitefish called *C.* (*Coregonus*) *clupeaformis* in Canada. In each of many lakes, including Lake Superior, it occurs in a single although variable form. But in each of a few widely separated lakes there are two sympatric species, both related to the humpback form but differing in gill-raker number from each other. Such sibling sympatric pairs occur where ciscoes are lacking because of natural barriers and the details of deglaciation.

In northwestern Maine, several lakes contain two related species of humpback whitefishes, one of which has higher gill-raker number and is dwarfed (Fenderson 1964). One example, Webster Lake, is indicated in Fig. 1. Again in Yukon Territory (some 4500 km distant), five or six lakes each contain two related humpback species, one a planktivore with high gill-raker number (Bodaly 1979). Three other such humpback sympatric pairs may have occurred in Canada before man's intervention: in Hanson Lake, Y.T., and in Dragon Lake near Quesnel, B.C. (both lakes poisoned by rotenone), and in Lake Opeongo, Ont. (Kennedy 1943) (in which one form had by 1968 become very scarce following the successful introduction in 1948 of the cisco *C.* (*Leucichthys*) *artedii*). The difference in gill-raker means

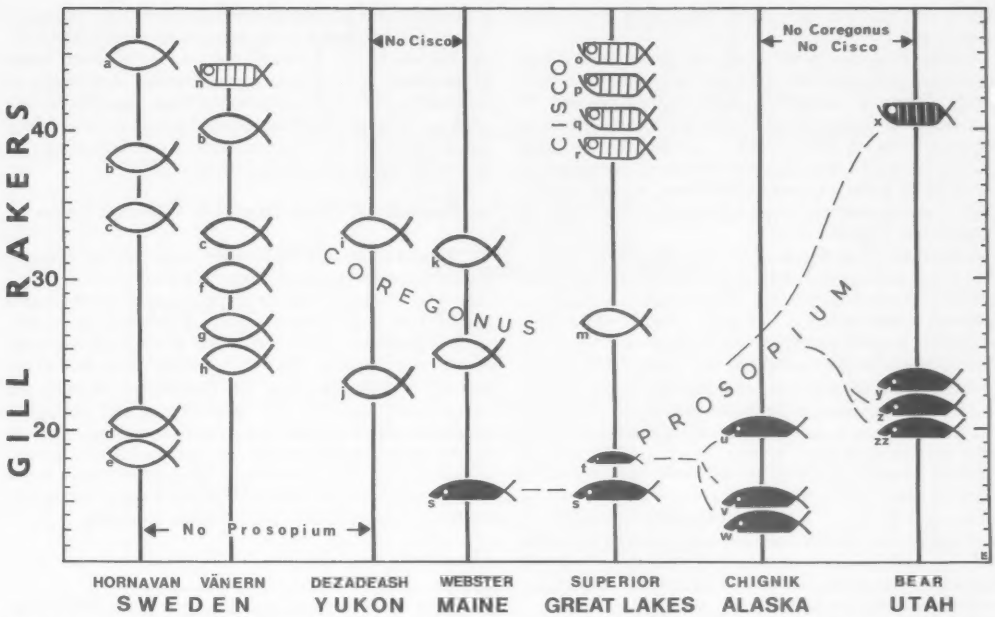

FIG. 1. Gill-raker numbers of coregonids in seven lakes. Each symbol represents the mean count of one species in that lake. *Coregonus* (*Coregonus*) open symbols are as follows: a, aspsik; b, planktonsik; c, blåsik; d, sandsik; e, storsik; f, storsik introgressed with blåsik; g, sandsik; h, älvsik; i, high-rakered Yukon form ("Squanga"?); j, low-rakered Yukon form; k, high-rakered Maine form; l, low-rakered Maine form; m, *C.* (*C.*) *clupeaformis*. *Coregonus* (*Leucichthys*) light-hatched symbols are as follows: n, *C.* (*L.*) *albula*; o, *C.* (*L.*) *artedii*; p, *C.* (*L.*) *hoyi*; q, *C.* (*L.*) *kiyi*; r, *c.* (*L.*) *zenithicus*. *Prosopium* black symbols are as follows: s, *P. cylindraceum*; t, *P. coulteri* of Lake Superior; u,v,w, *P. coulteri* of Chignik Lake (high-rakered, deep-water low-rakered, and shallow-water low-rakered forms, respectively); x, *P. gemmiferum*; y, *P. williamsoni*; z, *P. spilonotus*; zz, *P. abyssicola*.

between the high and low sympatric forms varies considerably between lakes within the Yukon Territory, and also within Maine (Fenderson 1964). (See next section.) Biochemical evidence demonstrates that although the high-rakered forms in all Yukon lakes may be monophyletic (Bodaly 1979), they must have developed independently from the high-rakered form in Maine (Lindsey et al. 1970). Apparently the high-rakered forms from widely different regions owe their similarity to convergence. All have as a common denominator the absence of any form of cisco, except in Tatchun Lake, where gill-raker numbers but not gill-raker lengths are the same.

Lake whitefishes are most speciose in Eurasia, where there are fewer species of *Leucichthys* and only one of *Prosopium* (and it does not reach Europe). In Sweden, with only two species of *Leucichthys*, there are at least six species of *Coregonus* (Svärdson 1979). (The vernacular rather than scientific names of Swedish whitefishes are used here because they are more stable.) Lake Hornavan contains five sympatric species, all in *Coregonus* (Fig. 1). Their gill-raker means span the whole range from 19 (comparable to most *Prosopium* elsewhere) up to 45 (comparable to many *Leucichthys* elsewhere). In this lake, the three species with highest gill-raker means are all planktivorous (Svärdson 1979, p. 42). In another Swedish lake, Vänern (Fig. 1), there are also three planktivorous species, but here one of them is a cisco *Leucichthys*. It is notable that in Sweden the most extreme planktivorous form of whitefish (*Coregonus*), the "aspsik," exceeds in gill-raker mean all Swedish populations of cisco (*Leucichthys*) (Svärdson 1979, p. 21; 1957, p. 356). In the only lake where the aspsik is sympatric with a cisco, the cisco is a dwarf of about 10 cm whereas the whitefish is large (35 cm) and has 11 more gill rakers than the cisco (Svärdson 1979, p. 22). Thus in Europe whitefishes evidently equal and even outdo ciscoes as plankton feeders, even though their external appearance is less obviously extreme.

Ciscoes reach their greatest diversity in the Great Lakes. Lakes Michigan and Huron each formerly contained eight sympatric species of *Leucichthys* (several of which are now endangered or extinct). Lake Superior contains at least four (Fig. 1). Among cisco species, there is some gradation in adaptation to plankton feeding; gill-raker means range from about 30 to 50, head profiles differ somewhat, and depth distribution and diet vary. Thus, the niches of the various species of ciscoes in North America seem comparable to those of the Swedish species of *Coregonus* that have raker means of 30 or more (Fig. 1) (except that some Great Lakes ciscoes are adapted to deep-water habitats lacking in Sweden). In North America, wherever ciscoes and lake whitefish are sympatric, the ciscoes have the higher raker count. But unlike *Coregonus* and *Prosopium*, *Leucichthys* has nowhere produced a form

with a very low gill-raker count nor a body form highly adapted to bottom feeding.

Turning to species in the genus *Prosopium*, these always have fewer gill rakers than sympatric species of other coregonids. There is usually a single species present, *P. williamsoni* in western North America or *P. cylindraceum* elsewhere in North America and in northern Asia. A dwarf species, *P. coulteri*, may occasionally occur in sympatry with one of these. It has a sporadic distribution, in Lake Superior (Fig. 1) and in scattered western North American localities (Lindsey and Franzin 1972).

In the Bristol Bay region of Alaska, pygmy whitefish occupy lakes on the margin of the unglaciated Bering refugium, and here they tend to diversify. Chignik Lake contains three sympatric forms related to *P. coulteri* (Fig. 2) which differ moderately in raker number. One is a plankton feeder, one a shallow-water benthic feeder, and one a deep-water benthic feeder. There is no other form of coregonid present (McCart 1970). Two other lakes in the Bristol Bay region, Aleknagik and Naknek, each contain just two sympatric forms which differ moderately in raker number. The taxonomic status of the three Chignik Lake forms is debatable, and may reflect either the outcome of sympatric divergence or of introgression following a period of allopatric divergence. Regardless of their origins, the Chignik Lake forms demonstrate the ability of the genus *Prosopium* to shift niches (with concomitant shift in gill-raker count) in the absence of competition from species of *Coregonus* or *Leucichthys*.

The most spectacular case of niche shift is also in the genus *Prosopium*, but in a water body of great antiquity. Bear Lake, on the Utah–Idaho border, lies in a valley probably continuously occupied by lakes since Pliocene times (Miller 1965). Here *Prosopium*, the only genus of coregonid present, comes in four species. One of these, *P. gemmiferum*, so remarkably resembles a cisco that it was still classified as *Leucichthys* by Hubbs and Miller in 1948. It is a small, elongate filter feeder with projecting lower jaw and 27–45 long gill rakers. Almost certainly a *Prosopium* because of its cranial osteology (Norden 1961), it is known from fossils to have already been differentiated from other species of *Prosopium* by Pleistocene time (Smith et al. 1968). The other three species have low raker counts (Fig. 1); two are endemic to Bear Lake and one, *P. williamsoni*, is widespread elsewhere and enters the lake from rivers only as an occasional migrant. Over a long span of time, and probably in the absence of any members of the genus *Coregonus*, *Prosopium* has in Bear Lake produced a species whose external morphology is more closely convergent on *Leucichthys* than that of any species of the subgenus *Coregonus* in Europe (where although the gill-raker counts are high, the head and body form are less modified).

In summary, where *Prosopium*, *Coregonus*, and *Leucichthys* occur together, their gill-raker means occupy the low, medium, and high portions, respectively, of the whole range of counts. In a few North American lakes where *Leucichthys* is absent, *Coregonus* shows a propensity to develop two sympatric forms, one adapted to the cisco niche. In northern Europe where *Prosopium* and *Leucichthys* are each few or absent, *Coregonus* species are much more diverse and span the whole range of raker counts. Where both *Coregonus* and *Leucichthys* are absent in North America, *Prosopium* shows a propensity (in Alaska) to develop two or three sympatric forms at the low end of the scale or (in the ancient Bear Lake in Utah) to develop sympatric species, one of which shows extraordinary convergence on the external morphology of *Leucichthys* elsewhere. Detection of these examples of convergence between species in different genera or subgenera is possible because there are conservative osteological characters which differentiate them.

Plasticity of Same Species in Different Lakes

Gill-raker count can vary between geographically separated populations that apparently belong to the same whitefish species. The biological species concept cannot be rigorously applied here as geographic separation precludes the test of whether members of two populations would interbreed were they to come together. The "same species" here rests on the subjective assumption that the populations included are monophyletic, and that such morphological and ethological differences as exist would not be sufficient to prevent their interbreeding if geography allowed. Morphological plasticity of such a group of populations can be examined either over a wide geographic range or between adjacent lakes. Variation is likely to be partly phenotypic and partly genotypic.

Continental Patterns

Species which were isolated in more than one Pleistocene refugium are likely to retain evidence of evolutionary divergence even after their postglacial dispersal. A clear example is *P. cylindraceum*, which has spread postglacially from two refugia, one in Beringia and one south of the Great Lakes area. Populations spreading from the two sources have not joined up, leaving a gap in the vicinity of Nelson River in northern Manitoba. Coincident with this distributional gap there is a sharp discontinuity in means (although not in ranges) of gill-raker counts and also of pyloric ceca (McPhail and Lindsey 1970, p. 112). Within each region populated from one refugium, there is clinal variation in climate but not in gill-raker number; between the two regions there is no great climatic difference but a sharp morphologic break. Therefore, the broad pattern of gill-raker variation is probably not due to phenotypic modification, but to genetic differences developed during isolation.

Coregonus clupeaformis also evidently survived both in the Bering and in a southeastern refugium. Although the ranges have rejoined postglacially, there is again a broad pattern in gill-raker means probably reflecting Pleistocene isolation (Lindsey et al. 1970). Corroboration is available from biochemical analysis (Franzin and Clayton 1977); discontinuities in isozyme frequencies coincide with watershed boundaries in a way supporting the hypothesis of genetically divergent stocks originating from at least two separate refugia. (A third refugium may have persisted in the Nahanni region of Northwest Territory (C. J. Foote, Department of Zoology, University of Manitoba, personal communication).)

No adaptive advantage has been attributable to particular alleles in this case, nor to particular gill-raker means in northern or southern refugia. In broad pattern, raker counts of Beringian populations tend to be lower than counts of southern populations in *C. clupeaformis*, but tend to be higher in

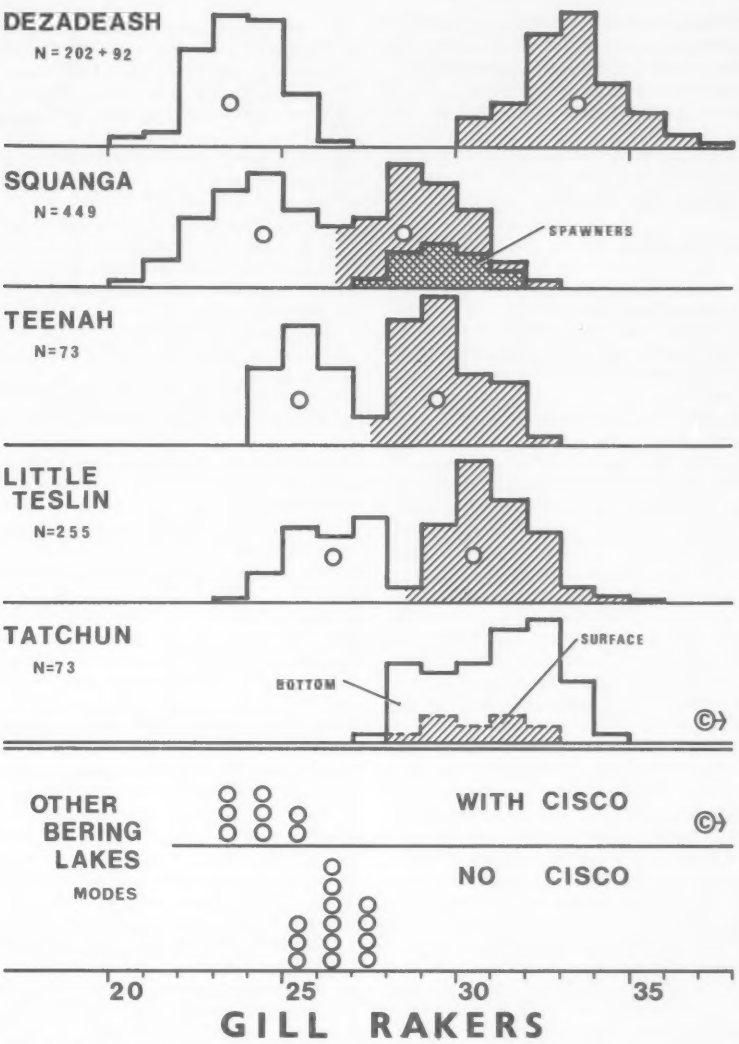

FIG. 2. Gill-raker numbers in five Yukon lakes each containing two sympatric forms of lake whitefish, and (bottom) in 21 other lakes in Bering Sea drainages each containing a single form of whitefish. Bars show frequency distributions of individual counts; circles show modal counts. "C" indicates presence of cisco *C.* (*L.*) *sardinella* with gill-raker modes near 45.

P. cylindraceum. Moreover, the continent-wide trend originating from glacial isolation tends to be partly obscured by considerable variation among populations in nearby lakes.

VARIATION WITHIN REGIONS

Some variation of one species between lakes is linked with the presence or absence of other species. The pygmy whitefish *P. coulteri* is know in British Columbia to exist in the absence of any other type of coregonid only in two lakes. In both lakes it has become a "giant pygmy whitefish," up to 28 cm long in contrast with under 15 cm everywhere else (McCart 1965, p. 1245). In these two lakes the gill-raker counts are above the average for other populations in those watersheds (although not for the whole range of the species). Zoogeographic evidence indicates that the differences must have arisen postglacially.

Some of the variation in gill-raker counts of

C. clupeaformis between lakes in the same region seems to be attributable to the presence or absence of ciscoes. Considering only lakes in Yukon Territory which contain unimodal populations of *C. clupeaformis*, gill-raker modes show a marked tendency to be lower if ciscoes are present than if they are absent (Fig. 2). This suggestion of an interdependence between ciscoes and whitefish is corroborated by the fact that it is only in lakes without ciscoes that the two distinct sympatric forms of lake whitefish occur.

Transfers between Lakes

Direct evidence of shift in the gill-raker count within a short time comes from the artificial transplanting of fish to new environments. One of the best documented cases involves Lake Maggiore in northern Italy, where man's intervention has evidently produced introgression at one time and character displacement at another.

No coregonids occurred in Lake Maggiore until the years 1860–80. During that period, two of the four whitefish species occurring sympatrically in Lake Constance (=Bodensee) were introduced into Maggiore. There they apparently hybridized, to form the "lavarello," with gill-raker count (31.3) intermediate between the counts of their parental forms (25.0 and 36.7) in Lake Constance (Fig. 3) (Dottrens 1959; Berg 1970).

In 1950 the "bondella," one of the two whitefish species occurring sympatrically in another lake, Neuchâtel (=Neuenburgersee), was also introduced into Maggiore. In its native lake, the bondella had a gill-raker count of 34.0, close to that of the lavarello in Lake Maggiore. In its new lake, the gill-raker count of the bondella rose by 3.7 within two or three generations (Fig. 3). Other morphological characters also shifted rapidly, so that the differences between bondella in Neuchâtel and in Maggiore are almost as great as the differences between bondella and lavarello in Lake Maggiore. Berg (1970) believes that the shift in gill-raker count "is too great to be interpreted as a phenotypical variation, but rather as a consequence of artificial and/or natural selection." The introduction in 1950 involved about 100 000 bondella fry. Gill-raker counts were already high in the 1959 year-class (Berg and Grimaldi 1965).

Svärdson (1957) also records shifts in gill-raker counts of transplanted whitefish. The älvsik is a whitefish species running into the Bure River from the Baltic Sea (where it is sympatric with a cisco species with high raker number). Transplanting älvsik into two small lakes which lacked ciscoes resulted in each case in a significant increase in gill-raker number. No differential mortality could be detected in gill-raker counts between transplanted fry and subsequent fingerlings (Svärdson 1952, p. 217), nor were increased gill-raker means due to sampling error nor apparently to water quality.

In another Swedish transplant, planting of one whitefish species from Lake Idsjön (where it had the highest raker count of three sympatric species) into a small lake with no native species produced a rise of 1.78 in gill-raker count along with a spectacularly increased growth (Svärdson 1952, p. 212).

In Canada, 100 000 eggs of *C. clupeaformis* collected from Lake Erie were transplanted in 1886 to Hogan's Pond in Newfoundland. Scott and Crossman (1964) report that in 1960 whitefish were still abundant in Hogan's Pond. Seventy-four years after the transplant, the gill-raker count was significantly higher (by 1.4 rakers) in the transplanted than in the donor population. Also in Canada, the second generation of lake whitefish (*C. clupeaformis*) which had been introduced into Lyons Lake were compared with their parental stock in Clearwater Lake (Loch 1974). Here the transplanted stock did not differ from the original stock in gill-raker number, but it did differ significantly in gill-raker length. There were several other differences, in gill-raker spacing, width, angle, and toothing (Tretiak 1975). Surprisingly, although phenotypes of Hb and lactate dehydrogenase did not differ, there was a difference ($P = 0.025–0.01$) in the proportions of L-glycerol-3-phosphate dehydrogenase between Lyons Lake and Clearwater Lake fish. Diet and limnological features differed widely in the two lakes; conceivably the observed isozyme difference may have been phenotypically induced (Loch 1974). Raker length may possibly also have varied directly in response to diet. Loch (1974) suggested that bottom organisms which were more abundant in the diet of the Clearwater Lake fish may have had an abrasive effect, but Tretiak (1975) rejected abrasion in favor of a dietary effect on raker development as a more likely hypothesis.

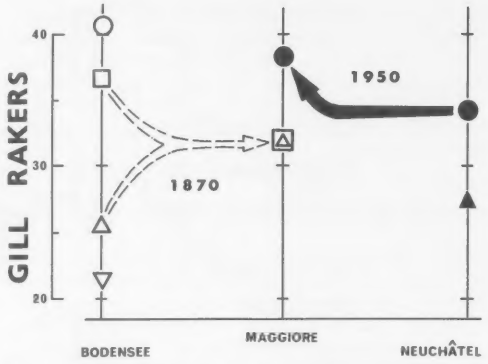

FIG. 3. Gill-raker means of two introduced coregonid stocks in Lake Maggiore, and of the stocks in their lakes of origin.

These studies on the effects on gill rakers of transplanting do not allow us to disentangle founder effects, rapid selection, and phenotypic responses, but they do demonstrate that even the supposedly conservative character of gill rakers can change in a very few generations.

Partial or Complete Introgression

A different source of lake-to-lake variation may be partial introgression, in those lakes containing closely related pairs. Among such lakes in Yukon Territory, Dezadeash has the two sympatric forms most sharply separated by raker counts (Fig. 2). In three other lakes (Squanga, Teenah, and Little Teslin), the raker means of the two forms differ by less. A fifth lake, Tatchun, was suspected on biochemical evidence of also harboring a sympatric pair. Unlike the preceding lakes, Tatchun does contain the least cisco *C.* (*Leucichthys*) *sardinella*. The two forms of *C. clupeaformis* are here indistinguishable by gill-raker number; they are still, however, bi-

modal with respect to gill-raker length, with the two forms tending towards slightly different diet and depth distributions (K. A. Martin, Department of Zoology, University of Manitoba, personal communication). Probably in the sympatric pairs of Yukon whitefish, the low-raker forms are monophyletic, on morphological (Bodaly 1979) and on biochemical grounds. The high-raker Yukon forms are probably also monophyletic (although of separate origin from the high-raker Maine forms). Treating all the Yukon high forms as one species, and all the Yukon low forms as another, one can see a gradation in degree of separation of the sympatric pairs, from no overlap in gill-raker characteristics (Dezadeash Lake) to virtual fusion (Tatchun Lake). The difference between lakes of either species is at least as great as the difference between the two sympatric species in each lake (except in Dezadeash). Similarly in Maine the difference between lakes of one species may be as much as the difference between some sympatric pairs of species in one lake (Fenderson 1964; Kirkpatrick and Selander 1979). Svärdson (1979) believes that even greater variation in gill-raker counts of allopatric populations in Swedish coregonids has arisen from partial introgression.

Differentiation within Lakes

In addition to the sympatric occurrence of two kinds of whitefish that are clearly behaving as two biological species, there are numerous instances of two or more distinguishable stocks of the same species occurring in the same lake. The morphological distinctiveness, and the extent of information available about such stocks, varies widely. Some are known to conform to the stock concept in that samples from different spawning aggregations can be distinguished on morphological or other grounds. Others may be morphologically distinguishable between different depths or different areas of a water body, but their segregation at spawning time is conjectural. (In the absence of samples of spawners, there is always the possibility that even though fish with different characteristics are associated with different habitats during nonreproductive periods, they may nevertheless mix during spawning.)

In Lake Winnipeg, spawning populations of *C. clupeaformis* can be distinguished in two major areas by gene frequencies of isozymes as well as by gill rakers and other morphological differences (Kristofferson 1978). Lake Superior contains more than one spawning stock of *C. artedii*, and also of *C. zenithicus* (Todd 1981). Different parts of Kootenay Lake, which have genetically distinct races of kokanee salmon (*Oncorhynchus nerka*) (Vernon 1957), probably also have separate spawning races of *P. williamsoni* (unpublished data).

In Lake Baikal there are three or more forms of *C.* (*Leucichthys*) *migratorius*, spawning in different rivers and differing in gill rakers, morphology, and ecology (Smirnov 1969). There are at least two sympatric populations of *C. albula* in Lake Ladoga, and in Lake Top, and elsewhere in Eurasia, and two of *C. peled* in several lakes (references in Behnke 1972, p. 663). In Lake Maggiore in Italy, there are small but significant differences between river-spawning and lake-spawning forms of one species (Berg and Grimaldi 1965).

Many other cases are known of morphological differences associated with spatial distribution within lakes. Kliewer (1970) found highly significant differences in gill-raker length (although not number) in *C. clupeaformis* from different areas of Lake Athapapuskow. Clarke (1973, p. 25) found differences in jaw length and profile in *C. artedii* from north and south ends of Montreal Lake, 30 miles (1 mile = 1.6 km) apart. Dymond (1926) stated that all species of cisco from one bay in Lake Nipigon had larger eyes than fish of the same species taken in the main body of the lake. Svärdson (1958) found much less divergence in gill-raker number between two sympatric *Coregonus* at one end of long narrow Lake Vojmsjön than at the other (which he attributed to partial introgression).

Morphological differences are often also associated with water depth. Dottrens and Quartier (1949, p. 727) found that one of the species of *Coregonus* (the "palée") in Lake Neuchâtel had a deep- and a shallow-water form, which differed in gill-raker numbers and other characters. Kliewer (1970) found a higher proportion of short-rakered *C. clupeaformis* in water with greater maximum depth. Hart (1931) found in *C. clupeaformis*, and Koelz (1929) in ciscoes, that fish taken in deeper water differed in body form and fin length.

Of great commercial interest is the existence of a dark, terete, soft-bodied form of *C. clupeaformis* in shallow areas of Great Slave Lake, Lake Athabaska, and elsewhere (Rawson 1947). These fish are more heavily infested with *Triaenophorus* than their deeper-water counterparts, and are commercially inferior. The proportion of such dark whitefish in the fisherman's catch on South Indian Lake in Manitoba has risen following the flooding of that lake, but it is unknown whether this resulted from a shift in the areas fished or possibly from a rise in the parasite incidence following enhancement of pike, the adult host. Dark whitefish may be a genetically distinct stock, or they may reflect phenotypic responses to parasitic infection, or shallow-water habitat, or both.

Finally, there are cases of bimodality in gill rakers within one species in one lake, but without information on spatial or spawning segregation. In an extensive survey, Clarke (1973) found suggestions of two or more sympatric forms of *C. artedii* in 26 central Canadian lakes. In nine of these the differences between the two forms were statistically significant. And the two forms in each were more similar to one another than to any other form (Clarke 1973, p. 173). Koelz (1929) also gave several examples of two forms of *C. artedii*, or of *C. hoyi*, within the same water body in the Great Lakes. Regardless of whether these cases of bimodality are from phenotypic or genetic causes, and regardless of whether they arose through allopatric or sympatric processes, their existence suggests that at least partially discrete sympatric stocks may occur commonly in coregonid fishes.

Phenotypic Variation

Gill-raker count in whitefish has been amply demonstrated by Svärdson (1958) to have a high genetic component. If whitefish are transplanted to a new lake, many features of the morphology of subsequent generations may be drastically changed and yet the gill-raker numbers may alter very little. Artificial selection of parental fish with extreme high or low raker numbers produces progeny with correspondingly high or low counts, and artificial crosses between whitefish species

produce hybrids with gill-raker numbers intermediate between those of their parents. From this experimental evidence there is little doubt that gill-raker count is under strong hereditary control.

Nevertheless, gill-raker number is evidently also subject to some direct phenotypic modification (although to a lesser extent than almost all other morphological characters which have been examined). Phenotypic effects may be suspected in some instances referred to in earlir sections, where raker number of a transplanted population changed quickly from that in the original environment, or where gill-raker number varied with depth or area of capture.

More direct evidence of phenotypic change comes from the observation that gill-raker count may sometimes differ significantly between year-classes. Thus, Hile (1937, p. 125) observed that among ciscoes of Silver Lake, the 1926 and 1928 year-classes differed significantly in gill-raker counts ($P < 0.01$). Berg and Grimaldi (1965) observed among bondella in Lake Maggiore a significant difference in gill-raker counts between year-classes, correlated to some extent with ecological conditions and growth rate in different years. The change in gill-raker length between parental and transplanted *C. clupeaformis* found by Loch (1974) has already been alluded to. (Kliewer (1970) also observed a correlation between gill-raker length and proportion of plankton in the diet of whitefish in adjacent lakes. In both the foregoing cases, the correlation might have been due to abrasion.) Koelz (1929, p. 539) compared 32 *C. clupeaformis* reared throughout life in the New York Aquarium with their parental stock from Lake Erie. The hatchery-reared fish had on average two fewer gill rakers than their parental stock, as well as longer heads, eyes, maxillae, snout, and paired fins. (Their gill-raker length was unchanged (Lindsey 1962, p. 708).) A striking case of modification by artificial rearing is described by McCart and Anderson (1967) in a salmonid; *O. nerka* reared in aquaria had four fewer gill rakers than their naturally reared relatives.

Another source of variation in gill-raker number relates to the length of the fish. Gill-raker number increases asymptotically in young fish, but the size at which the final (adult) number is reached may vary between localities and is perhaps subject to environmental influence. Gill-raker length relative to body length may change continuously throughout life, and also depend on the environment (Kliewer 1970, p. 158).

In summary, gill-raker differences between populations are not necessarily purely genetic. Gill-raker count does not seem to be subject to the same amount of drastic phenotypic modification as are other meristic counts or body proportions in whitefish. Nevertheless, moderate differences in gill-raker number, such as may be used to differentiate stocks within one water body, could reflect direct environmental influences.

Gill Rakers as Stock Markers

This survey has concentrated on gill-raker count, the character most used for taxonomic discrimination in coregonids at all levels from stocks to genera. All other characters (except perhaps biochemical ones) are less reliable as "markers" of genetic similarity as they are bedeviled by an immense phenotypic plasticity. Hence any cautions emerging from a survey of gill-raker characteristics must be applied even more strongly to the use of other morphological characteristics.

Transplants have shown that gill-raker counts can shift rapidly and significantly. There will be many biotic and abiotic differences between the old and new environments, whose effects on gill rakers are not easily disentangled. By looking at different degrees of taxonomic and geographic divergence, some of these effects can be separated.

Apparently gill-raker number responds strongly to the presence or absence of other related species. The apparent principle, referred to in the introduction, is that gill-raker counts expand so as to fill available niches. This fine tuning between cohabiting species can be attributed to sharp selective forces acting on a character which demonstrably has a high hereditary component. The effect is strongly evident in the comparisons of regions in which one or other of the three major taxonomic groupings *Prosopium, Coregonus,* and *Leucichthys* are missing. The striking examples of character shift (e.g. the ciscolike *Prosopium* in Bear Lake where there is no other planktivore) probably occurred over a very long time. But there seems to be a continuum between these and the lesser shifts in raker number occurring over a shorter period. The difference between whitefish gill-raker counts in Yukon lakes with and without ciscoes must have developed within 10 000 yr. The causes of the small but significant gill-raker shifts described in recently transplanted populations probably differ only in degree but not in kind from the causes of the larger and older differences.

Because gill-raker count of a population is apparently sensitive to the presence of other species, it follows that the introduction into a lake of a new species may cause a change in gill-raker number of species already present. Some coregonids in the Great Lakes may have shifted their gill-raker number in response to the advent of smelts or alewives or kokanee. Alternatively, reduction or extinction of one species for whatever cause may allow a surviving species to shift over in the gill-raker spectrum to exploit a vacated feeding niche.

The underlying assumption is that competition for food drives the gill-raker adjustments. If so, changes in abundance or nature of food arising from causes other than addition or subtraction of competitor species might also produce a gill-raker shift. Eutrophication, or introduction of new food organisms, could be followed by changes in gill-raker counts.

Changes in gill-raker number can arise from introgression, to which coregonid species are particularly prone. Hybrids can be created readily by artificial crossing, even between pairs of coregonid species which are morphologically very different. Mass hybridization may follow man-made introductions (as in Lake Maggiore), or may be induced by man-made alteration of the environment (Svärdson 1979, p. 60). Cases of spontaneous hybridization even between *Coregonus* and *Leucichthys* are know in several countries. Svärdson attributes the diversity of European populations to various degrees of introgression between a relatively small number of ancestral types.

When hybridization between two original forms is total, the result is a single intermediate form which can be treated as one stock. But when introgression is only partial, with some bimodality retained in the presence of some gene flow between the two modes. then problems arise in applying the stock concept. The series of pairs of sympatric species in lakes in

Yukon Territory, and again in Maine, suggest various degrees of balanced partial introgression. Alternative evolutionary mechanisms, however, could be involved. Sympatric speciation may have occurred independently and progressed to a different degree in each lake. (Biochemical evidence, although inconclusive, does not support this view.) The same two allopatrically evolved forms may have secondarily contacted each other in each lake, and are in different stages of a process of total introgression which will eventually produce a unimodal population in each lake. (Tatchun Lake would be most advanced in this process.) As a variant on the preceding suggestion, character displacement rather than introgression may be in the process of driving sympatric pairs into greater divergence (in which case Dezadeash Lake would be most advanced). Or, a steady state may exist in each lake, with gill-raker counts tuned to the particular niches available there (or with a balance, separately struck in each lake, between gene leakage and selection). Whatever their evolutionary background, these series of sympatric pairs with varying divergence do not comfortably fit the stock concept. If they are due to varying degrees of gene flow between the sympatric pairs of populations, then there seems no objective boundary between population pairs which are behaving as two stocks and those which are not.

The management of two sympatric (or parapatric) "stocks" showing balanced partial introgression would require knowledge of the amount of gene flow and how it might change with alteration in the population parameters of each stock. For example, in Tatchun Lake it would be difficult to predict what effect a change in fishing mortality on just one of the two poorly differentiated "stocks" might have on the other. As an analogy, two populations of rainbow trout spawn in inlet and outlet streams of Loon Lake, British Columbia (Lindsey et al. 1959). The proportion of the progeny from each stream which stray as adults to the other stream is the same (6%), but because the inlet-spawning population is about four times as numerous, the outlet run in each year is composed 25% of strays whereas the inlet run has only 1% strays. Hence removal of a given number of fish from the outlet-spawning population would have a much greater effect on hybridization than would removal of a comparable number of fish from the population which spawns in the inlet. In the sympatric pairs of Yukon coregonids, the difference between lakes in degree of introgression may depend partly on their relative population sizes, and could be expected to change in response to altered fishing pressures.

A final chameleonlike feature of coregonid, and indeed all, fishes is their susceptibility to morphological change in response to direct environmental influence. Change in morphology with time, or with distance, does not necessarily imply genetic difference (nor of course preclude it). However, morphological bimodality could still be an indicator of the presence of two stocks even though phenotypically induced, provided there is segregation of spawners into two places or times where different environmental conditions then produce phenotypic bimodality. But bimodality must be observed between samples of separately spawning adults, demonstrating that segregation of the modes actually occurs during reproduction. In the absence of this evidence, bimodality of nonreproductive individuals may simply reflect phenotypic responses to two sets of environmental conditions in two spawning sites.

It has not been the intention of this paper to suggest that in studies of coregonid stocks gill-raker counts should be abandoned. On the contrary, gill-raker counts are less prone to environmental modification, and are therefore more useful, than any other known morphological character. They can, however, respond quite quickly to changes in the biological surroundings, probably because the number of gill rakers is directly related to feeding efficiency and is therefore subject to stringent selection.

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Use of Allelic Frequencies to Describe Population Structure[1]

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ALLENDORF, F. W., AND S. R. PHELPS. 1981. Use of allelic frequencies to describe population structure. Can. J. Fish. Aquat. Sci. 38: 1507–1514.

Development of electrophoretic techniques has allowed the estimation of allelic frequencies at many isozyme loci in populations of fish. The pattern of allelic frequency divergence in salmonid populations has been used to describe the pattern of genetic exchange and degree of isolation among local geographic units. Our goal is to determine how much genetic exchange among subpopulations will yield observed patterns of allelic divergence. We approach this goal using population genetics theory and a series of computer simulations.

The amount of allelic divergence between subpopulations is a function of the absolute number of migrant individuals exchanged, and not the proportion of individuals exchanged. Therefore, some knowledge of population sizes is needed to estimate degree of reproductive isolation from allelic frequency data. Second, statistically significant allelic divergence will often be present even when there is substantial exchange among subpopulations. For example, significant allelic divergence was present in our simulations over 50% of the time with 20 subpopulations exchanging 50 individuals per generation. Third, allelic frequencies estimated from fry should be used with caution when drawing conclusions about the significance of allelic divergence in the reproducing adults.

Key words: allelic divergence, reproductive isolation, gene flow, genetic drift, computer simulations

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Grâce aux techniques électrophorétiques, il a été possible d'estimer les fréquences alléliques à plusieurs loci d'isozymes chez des populations de poissons. On a utilisé les divergences de fréquences alléliques chez des populations de salmonidés pour décrire les échanges génétiques et le degré d'isolement parmi des unités géographiques locales. Notre objectif était de déterminer jusqu'à quel point un échange génétique entre des sous-populations résultera – des caractéristiques observées de divergences alléliques. A cette fin, nous faisons appel à la théorie de la génétique des populations et à une série de simulations sur ordinateur.

Le degré de divergence allélique entre sous-populations est fonction du nombre absolu des individus migrateurs échangés et non de la proportion d'individus échangés. Il faut donc avoir une certaine connaissance des effectifs d'une population si l'on veut estimer le degré d'isolement reproducteur à partir de données de fréquences alléliques. En outre, il y aura souvent divergence allélique significative à l'analyse statistique, même s'il y a échange substantiel entre sous-populations. Comme exemple, dans nos simulations, nous avons trouvé une divergence allélique significative dans plus de 50% des cas, avec 20 sous-populations échangeant 50 individus par génération. Enfin, les fréquences alléliques estimées à partir des alevins devraient être utilisées avec prudence quand on tire des conclusions relatives à la signification de la divergence allélique chez les adultes reproducteurs.

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FISHERIES biologists have long been interested in genetic differences between populations of salmonids. Showing the hereditary basis of such differences, however, has presented problems. Characteristics such as growth rate, age at maturity, coloration, meristic counts, and morphometric measurements are all affected to an unknown extent by environmental influences. Detailed studies using controlled environmental conditions are necessary to demonstrate that differences between stocks do have a genetic basis. Ricker (1972) presented an extensive review of hereditary differences between salmonid populations. The evidence for a

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genetic basis of most of these differences was largely circumstantial. Simon (1972) in the same volume had to fabricate allelic frequencies for chinook salmon (*Oncorhynchus tshawytscha*) from the lower Columbia River in his presentation because actual allelic frequencies were not available.

A mountain of data on protein variation has become available in the last 10 years for practically all major salmonid stocks throughout the world by the use of electrophoresis. A great deal of effort has been spent verifying the inheritance of electrophoretic polymorphisms used in population studies of salmonids (Allendorf and Utter 1973, 1976; Allendorf et al. 1975; Aspinwall 1973, 1974a; Bailey et al. 1970; Clayton et al. 1973, 1975; Eckroat and Wright 1969; May et al. 1975, 1979a, b, 1980; Morrison 1970; Morrison and Wright 1966; Reinitz 1977a, b; Ropers et al. 1973; Stoneking et al. 1979; Utter et al. 1973, 1979; Wright et al. 1975, 1980). Thus, we now have at hand an enormous quantity of allelic frequency data describing genetic variation in salmonid populations.

How can these data be applied to further our understanding of the genetic structure of salmonid populations? The primary goal of most genetic studies of salmonid populations is to describe the pattern of genetic exchange and isolation among geographic units. The pattern of genetic divergence in natural populations results from the action of three basic evolutionary forces: migration, genetic drift, and natural selection. Thus, we should have an understanding of the effects of natural selection on the loci studied to interpret observed allelic frequencies in terms of migration patterns and genetic drift.

It has been notoriously difficult to estimate the effects of natural selection on genotypes at individual loci. In fact, it is still under debate whether the allelic variation of proteins detected with electrophoresis results from the action of natural selection or selectively neutral mutations and genetic drift. A number of studies of fish populations have presented evidence that at least some polymorphic protein loci in fish are under the influence of selection (Christiansen 1977; Fujino and Kang 1968; Johnson 1971; Koehn and Williams 1978; Mitton and Koehn 1975; Place and Powers 1979). However, evidence has also been presented that selectively neutral mutations, genetic drift, and genetic exchange between populations, rather than selection, are of primary importance in producing allelic variation of proteins in fish (Allendorf 1978; Aspinwall 1974b).

There is thus a fundamental problem in the use of allelic protein variants to describe population structure (i.e. the subdivision of a species into local interbreeding units). We can now readily estimate allelic frequencies at many loci in natural populations. Allelic frequencies are determined by natural selection and migration patterns, one of which is unknown and the other we are trying to estimate. The way out of this dilemma is to ignore natural selection; we assume that the patterns of allelic frequencies we observe are determined by migration and genetic drift. There are several reasons for accepting this assumption. The primary one is that there are many possible models of selection to consider and no empirical basis for choosing among them. Also, if selection was having a strong influence on these loci, the controversy about the importance of natural selection would have been resolved long ago. In addition, different loci usually provide similar estimates of divergence, as expected under the neutral model. If each locus was affected by its own regime of selection, then we would not expect such uniformity.

The usual procedure used to describe population structure is to estimate allelic frequencies at many loci in a series of population samples from a species. Assume the alleles are unaffected by natural selection. Then interpret the observed pattern of genetic relationships in terms of the amount of genetic exchange between groups.

In this paper we examine how much genetic exchange among population units will yield observed patterns of allelic divergence. This step in the process is often an exercise in intuition. The basis of these interpretations comes from the rich theory available in the discipline of population genetics. A basic 'rule of thumb' is that very little genetic exchange between populations will prevent divegence in the absence of natural selection. It is accepted that "migration at the rate of one migrant individual per local population per generation is, generally, sufficient to obscure any disruptive effects of drift" (Spieth 1974).

This principle is correct but has been inappropriately applied in analyzing population structure at a single point in time. One migrant per generation is sufficient to ensure that the same alleles will be shared over long periods of evolutionary time. But, one migrant is not sufficient to maintain identical allelic frequencies between populations.

The standard measure of divergence at individual loci among subpopulations (F_{ST}) was defined by Wright (1943)

$$(1) \quad F_{ST} = \frac{\sigma_q^2}{\bar{q}\,(1 - \bar{q})}$$

where $\bar{q}$ and σ_q^2 are the mean and variance of allelic frequencies among subpopulations. Lower values of F_{ST} indicate less genetic divergence. Nevertheless, as pointed out by Wright (1969), "a rather small value of F may be associated with a very considerable amount of differentiation among the subpopulations."

The goal of this paper is to determine what can be inferred about the rate of genetic exchange among subpopulations on the basis of allelic frequency data. We do this using population genetics theory and a series of computer simulations.

The Model

Consider a diploid population composed of 20 subpopulations (demes or local random mating units), each with a population size of N. Each generation an individual has probability m of breeding in a subpopulation other than that of his birth. We assume that an emigrant is equally likely to immigrate into any of the other subpopulations (the 'island model' of migration). This model is appropriate to simulate a population of salmonids inhabiting a lake, the population being divided into a series of subpopulations representing different spawning aggregations.

Changes in allelic frequencies are modeled by a Monte Carlo simulation using different values of m and N. Four uniformly distributed (0−1) pseudorandom numbers are used to select each zygote. The first pseudorandom number determines whether the gamete comes from the parent subpopulation or is an immigrant. The second number determines the allele selected. This process is then repeated to form a

TABLE 1. Simulation results of steady-state F_{ST} values with 20 subpopulations for different population sizes. Each value is the average of 20 repeats.

	mN						
	0.5	1	2	5	10	25	50
$1/(4mN + 1)$	0.3333	0.2000	0.1111	0.0476	0.0244	0.0099	0.0050
$N = 50$	0.2956	0.1826	0.1077	0.0484	0.0264	0.0120	—
$N = 100$	0.3350	0.1884	0.1061	0.0437	0.0251	0.0095	0.0061
$N = 200$	0.3216	0.1963	0.1037	0.0531	0.0237	0.0106	0.0053

zygote. This is completed for N new zygotes for the next generation. The initial allelic frequency in each subpopulation is 0.5, and there are no differences in fitness among the three genotypes. This model does not include the effects of mutation.

Results

DIVERGENCE AT STEADY STATE

Wright (1969) has shown that at equilibrium with the island model of migration and an infinite number of subpopulations

$$(2) \quad F_{ST} = (1 - m)^2/[2N - (2N - 1)(1 - m)^2].$$

If m is small this approaches the more familiar

$$(3) \quad F_{ST} = 1/(4Nm + 1).$$

Nei and Chakravarti (1977) have shown that with a finite number of subpopulations F_{ST} becomes 0 because all subpopulations eventually become fixed for the same allele. We ignore this effect, however, assuming that in nature some migrants will be entering our 'closed' system from the outside. In the finite subpopulation model, F_{ST} and the allelic frequency distribution will eventually reach some steady-state decay distribution (Nei et al. 1977). The expected steady-state values of F_{ST} decrease as the number of subpopulations decreases (Li 1976). The decay to $F_{ST} = 0$ will be extremely slow in our simulations where the total population size is 1000−4000. We have taken this effect into account in presenting our simulations results by using steady-state values (as defined in the next section) to describe divergence among subpopulations.

The critical point of formula (3) is that the amount of divergence among subpopulations is a function of the absolute number of migrant individuals (mN), and not the proportion of exchange among subpopulations (m). Thus, we expect to find the same amount of genetic divergence among subpopulations of size 1000 with 2.5% straying as with subpopulations of size of 50 with 50% straying. Fisheries managers and ecologists are likely to be interested in the proportional amount of exchange among subpopulations; allelic frequency data alone are at best capable of estimating the number of individuals straying. Estimates of effective population sizes are thus also needed. Unfortunately, it is extremely difficult to estimate the effective population size of natural populations.

The dependence of divergence on the number of migrants, rather than the proportion of migrants, may at first seem counter-intuitive. The rate of divergence, however, results from the opposing forces of migration and genetic drift. The larger the subpopulations are, the slower they are diverging

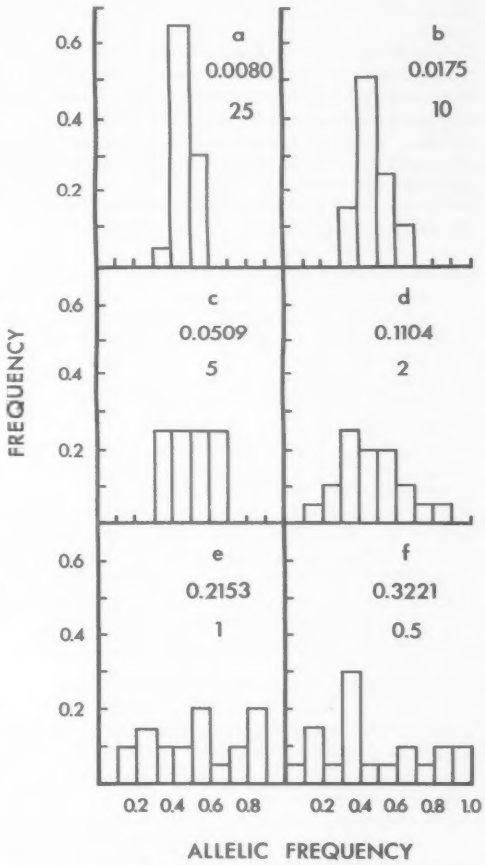

FIG. 1. Distribution of allelic frequencies in 20 subpopulations (N = 200) with different amounts of migration. The number on each graph is the value of F_{ST} for that distribution. (a) mN = 25; (b) mN = 10; (c) mN = 5; (d) mN = 2; (e) mN = 1; (f) mN = 0.5.

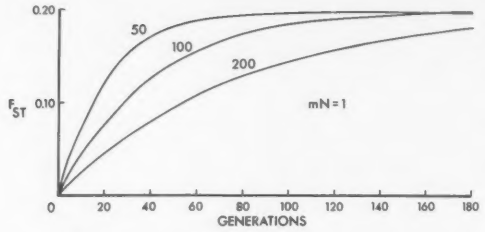

FIG. 2. Expected increase of F_{ST} using formula (4). The value of N is shown above each curve.

through drift; thus, proportionally fewer migrants are needed to counteract the effects of drift. Small subpopulations diverge rapidly through drift, and thus proportionally more migrants are required to counteract drift.

Table 1 shows that the values of F_{ST} predicted by formula (3) are closely realized with our simulations for three population sizes and a variety of values of mN. Figure 1 shows the distribution of allelic frequencies seen with the first repeat of each migration rate with $N = 200$.

RATE OF APPROACH TO STEADY STATE

Wright (1951) has derived the following recurrence equation for F_{ST} with an infinite number of subpopulations:

$$(4)\quad F_{ST}^{(t)} = (1 - m)^2\left[\frac{1}{2N} + \left(1 - \frac{1}{2N}\right)F_{ST}^{(t-1)}\right]$$

where $F_{ST}^{(t)}$ is the value of F_{ST} in the tth generation. The rate of approach to steady state is dependent upon m (Fig. 2), rather than just mN. Smaller subpopulations, with larger values of m, reach steady state much more quickly for a given value of mN. This effect is seen clearly in our simulations (Table 2). Doubling the subpopulation size approximately doubles the time to steady state. We estimated steady-state values of F_{ST} by our simulations at $2(T_{0.90})$ generations, where $T_{0.90}$ is the number of generations at which $F_{ST}^{(t)} = 0.90\,[1/(4mN + 1)]$ using formula (4).

DETECTING DIVERGENCE IN NATURAL POPULATIONS

How much divergence must be present before we detect statistically significant heterogeneity in our samples? A common procedure is to sample 50 or so individuals from each suspected subpopulation and then apply some standard test, such as contingency χ^2 analysis, to detect heterogeneity. We can do this with our simulations by sampling 100 genes from each subpopulation and then applying a 2×20 contingency χ^2 (df = 19) on alleles observed in our sample (Table 3).

Statistically significant divergence pattens are often associated with low F_{ST} values and fairly high migration rates. For example, even with a mN value of 25, significant divergence is detected 60% of the time with a significance level (α) of 0.05. In fact, significant heterogeneity may often be present under certain conditions (low N) when there is no isolation.

This effect is more clearly discussed for the case of just two subpopulations. Imagine a population of trout inhabiting a lake. There are two spawning aggregations (subpopulations), one in the inlet stream and one in the outlet stream. How do we determine if the two subpopulations are reproductively isolated from each other? We can take samples of fry from both streams, analyze them at several electrophoretic loci, and test to see if we should reject the null hypothesis that our two samples are drawn from the same population.

There is a fundamental error in this approach. Assume that fish in the lake move to the spawning areas completely at random; that is, their location of birth has no effect on where they spawn. Let us consider a locus having two alleles (A,a) with an allelic frequency P for the A allele for the fish in the lake. The groups in the two spawning areas have frequencies at this locus of $P1$ and $P2$, with a variance of $(P(1 - P)/2N)$. We then sample some 50 fry from each area to provide estimates ($\hat{P}1$ and $\hat{P}2$) of $P1$ and $P2$. A statistical procedure is then applied to test if $P1 = P2$. The problem is that $P1$ and $P2$ are likely to be different, not because of any reproductive isolation, but simply because of the finite number (N) of spawners in each subpopulation.

Consider the mathematically extreme case of $N = 1$. The probabilities of the three possible parental genotypes for each subpopulation are P^2, $2PQ$, and Q^2 for AA, Aa, and aa. Allelic frequencies in the two subpopulations can only be 0.00, 0.50, or 1.00. We are certain to reject the null hypothesis with our sample of 100 genes from the progeny, except when both subpopulations have indentical allelic frequencies. Therefore, we will not detect a significant difference approximately $[(P^4) + (1 - \alpha)(4P^2Q^2) + (Q^4)]$ proportion of the time. For $\alpha = 0.05$, $P = 0.5$, and $N = 1$, we expect to detect a significant difference ~64% of the time.

Thus, even if fish are returning at random to spawn, there is an inflated probability to detect a significant difference between $\hat{P}1$ and $\hat{P}2$. The probability of detecting a significant difference will depend on N. If N is very large, then $P1 = P2$

TABLE 2. Simulation results of the generations required to reach expected $[1/(4mN + 1)]$ values of F_{ST} with 20 subpopulations. Each value is the median among 21 repeats.

	mN						
N	0.5	1	2	5	10	25	50
50	63	32	25	8	7	2	—
100	142	79	54	25	11	6	2
200	287	171	95	41	27	12	4

TABLE 3. Simulation results showing proportion of 20 repeats in which significant ($\alpha = 0.05$) genetic divergence was detected sampling 100 genes from each of the 20 subpopulations at steady-state values of F_{ST}.

	mN					
N	0.5, 1, 2, 5	10	25	50	75	100
50	1.00	0.95	0.60	—	—	—
100	1.00	0.90	0.65	0.60	0.30	—
200	1.00	1.00	0.70	0.60	0.40	0.35

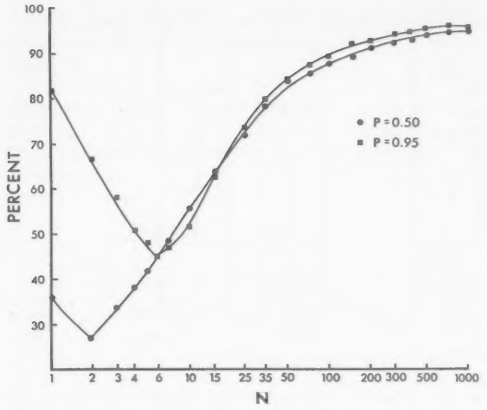

FIG. 3. Simulation results showing proportion of the time that we did not detect significant allelic divergence in the progeny between two subpopulations each derived from N adults that were sampled at random from a single population with allelic frequency P. Fifty progeny (100 genes) were sampled from each subpopulation and significance was tested with a 2×2 χ^2 contingency test. Each point represents the percent of 2000 repeats in which $\chi^2 < 3.84$.

and we will detect significance, using the $\alpha = 0.05$ criterion, the expected 5% of the time. This probability will increase as N becomes smaller. We have used simulations to determine this relationship using a 2×2 contingency χ^2 and determining what proportion of the time we do detect a significant difference between $\hat{P}1$ and $\hat{P}2$ when the fish are returning at random to the two subpopulations (Fig. 3). As expected, when N is large (1000) we reject the null hypothesis 5% of the time. For values of N less than 100, however, there is a greatly enhanced chance of rejecting the null hypothesis. For example, when $N = 50$ and $P = 0.5$, we detect divergence ~15% of the time. This effect is largely independent of allelic frequency except when N is very small (less than 10).

The problem is that we are trying to draw conclusions about the spawning populations by examining their progeny. We cannot do this without knowing the effective population sizes of the subpopulations. The correct way of approaching the question of possible genetic differences between subpopulations is to sample the spawners. This is presently a realistic alternative only with species such as Pacific salmon that die after reproduction.

This effect should not readily be dismissed. Lacustrine populations are often divided into a number of spawning subpopulations, some of which may reproduce in small streams. Samples for electrophoresis are usually collected from young fish that are much more abundant than spawners. Significant heterogeneity may be generated by our sampling scheme, rather than by any isolation among subpopulations.

To examine further these effects we have carried out another series of simulations that are identical except that there are only two subpopulations. These simulations make it much easier to see the relationship between population size, migration rate, detection of allelic frequency divergence, and temporal stability.

Table 4 summarizes the simulation results in the case of two subpopulations. We see the same major effects present as in the case of 20 subpopulations, i.e. significant allelic frequency differences even with fairly high migration rates. The proportion of repeats with significant divergence is lower with two subpopulations. With only two subpopulations there is a reasonable probability of allelic frequencies being similar by chance alone. Also, with fewer subpopulations a higher proportion of genes are exchanged with each individual subpopulation for the same value of m.

We do not expect allelic frequency differences generated largely by small N, rather than by reproductive isolation (i.e. small m), to be temporally stable. For example, Fig. 4 shows the changes in allelic frequencies over many generations for two N values having the same mN, and thus the same amount of divergence. The allelic frequencies are obviously more stable with larger N values. This difference is probably not detectable by actual empirical study of salmonid populations; generation time is too long and our scientific lifetimes too short. One possibility, however, is the study of pink salmon populations that have a rigid 2-yr life cycle.

Discussion

How should we describe population structure using allelic frequency data from natural populations of salmonids? The best study that we are aware of is with sockeye salmon (*O. nerka*) from Lake Azhabach'e in the Kamchatka River drainage by Altukhov and his colleagues (Altukhov et al. 1975a, b). Spawning adults were sampled from 27 subpopulations over a 3-yr period and typed at two polymorphic loci (Ldh and Pgm). Counts of total male and female spawners in each locality were also made to estimate the effective population size of each subpopulation.

Our present analysis is restricted to the samples collected in 1972, when 20 subpopulations and over 1000 fish were sampled. The estimated average effective population size per

TABLE 4. Simulation results with two subpopulations showing proportion of 50 repeats in which significant ($\alpha = 0.05$) genetic divergence was detected sampling 100 genes from each subpopulation. Only cases where at least one subpopulation remained polymorphic (frequency of common allele less than 0.95) are included.

	mN							
N	0.25	0.50	1	2	5	10	25	50
50	0.84	0.82	0.64	0.42	0.36	0.20	0.14	—
100	0.80	0.78	0.72	0.54	0.40	0.22	0.12	0.00
200	0.84	0.80	0.62	0.50	0.36	0.22	0.12	0.12

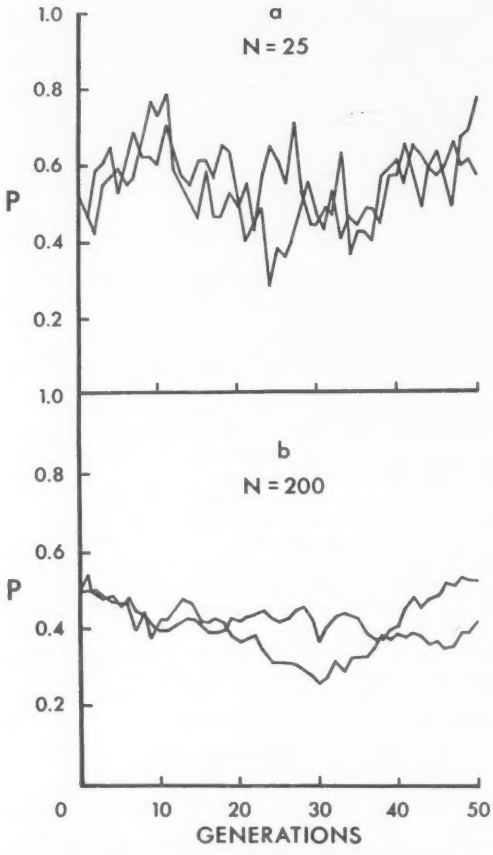

FIG. 4. Simulation results showing change in allelic frequencies in two subpopulations with an exchange (mN) of five individuals per generation. (a) $N = 25$ and $m = 0.2$; (b) $N = 200$ and $m = 0.025$.

subpopulation is ~200. The F_{ST} values for Ldh and Pgm are 0.0202 and 0.0106, respectively. Significant allelic frequency divergence was present only at the Ldh locus ($\chi^2_{19} = 37.53$, $P < 0.01$).

How much migration among subpopulations is compatible with the observed divergence? If we solve formula (3) for the observed F_{ST} values at Ldh and Pgm, we estimate mN values of 12.1 and 23.3. Are these two estimates of the number of migrants significantly different? We can answer this by determining if these two patterns of divergence are compatible with a single model of population structure. The average observed F_{ST} value of these two loci is 0.0154, which yields an mN value of 16.0 with formula (3). We simulated 200 repeats using these values ($N = 200$, $mN = 16.0$) in our model to determine the distribution of F_{ST} values (Fig. 5). The patterns of divergence at both loci are compatible with this amount of migration; 23% of the simulated F_{ST} values are less than the F_{ST} for Pgm, and 16% are larger than the F_{ST} value for Ldh.

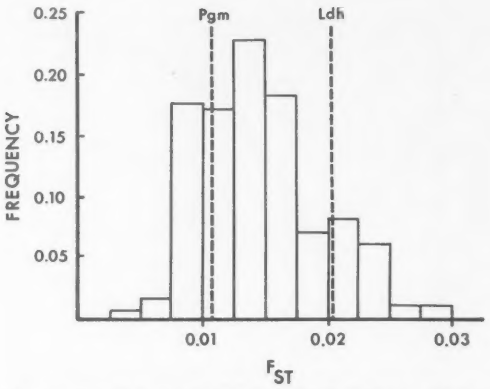

FIG. 5. Simulation results showing distribution for F_{ST} values in 200 repeats for $N = 200$ and $m = 0.08$ with 20 subpopulations. The dotted lines show the F_{ST} values actually estimated by Altukhov et al. (1975b) for the Pgm and Ldh loci.

Thus, the observed patterns of allelic divergence are both compatible with 8% straying among subpopulations, with an island model of migration and selectively neutral alleles. This 8% is actually a conservative estimate. If there is a tendency for individuals who stray to reproduce in adjacent subpopulations ('isolation by distance'), then more migration will produce the same amount of divergence. This results from there being increased exchange between subpopulations that are genetically similar. Therefore, each migrant is less effective in retarding divergence because it has an increased probability of reproducing in a subpopulation that is similar to the one from which it emigrated.

The importance of examining many polymorphic loci can be seen from this example. A single estimate of F_{ST} would be compatible with an extremely wide range of migration values. As each additional locus and estimate of F_{ST} is added, we narrow the possible range of migration values that are compatible with our observations.

Conclusions

There are three major points that we believe deserve special emphasis. The first is that the amount of divergence among subpopulations is a function of the absolute number of migrants exchanged. Therefore, allelic frequency data alone cannot be used to estimate the proportional amount of exchange among subpopulations. An exchange of 25 migrants between subpopulations will result in the same amount of divergence whether those 25 represent 1% or 50% 'straying' between subpopulations. Some knowledge of effective population sizes is required to estimate proportional rates of exchange from allelic frequency data.

Second, statistically significant patterns of allelic divergence are often present even when there is considerable exchange among subpopulations. Therefore, the finding of significant allelic divergence should not be interpreted to imply the exchange of very few individuals among subpopulations. With 20 subpopulations, an exchange rate of 10 individuals will almost always result in significant di-

vergence, and an exchange rate of 50 individuals will result in significant divergence approximately one-half of the time (Table 3).

Third, it is dangerous to draw conclusions about reproductive isolation between adults by estimating allelic frequencies in their progeny. Differences caused by a small number of reproducing adults without any reproductive isolation can become highly statistically significant when a large number of progeny are sampled.

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The Stock Concept and the Uncoupling of Organismal and Molecular Evolution[1]

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CLAYTON, J. W. 1981. The stock concept and the uncoupling of organismal and molecular evolution. Can. J. Fish. Aquat. Sci. 38: 1515–1522.

Evidence in support of the view that molecular evolution proceeds at a steady rate is presented in a brief review. This view of the steady rate of evolution of structural proteins, known as the molecular clock hypothesis, is shown to apply to the kinds of proteins that are commonly examined for variation by means of electrophoretic and immunological techniques in investigations of the stock structure of populations. The review is extended, with examples from the ichthyological literature, to show that the pace of organismal evolution is quite erratic in comparison to the pace of molecular evolution. A resolution of the apparent paradox regarding the uncoupling of the course of molecular and organismal evolution is offered based on the published suggestion of Allan C. Wilson and colleagues that the molecular divergence of any pair of populations should be seen as representing a time scale for the divergence. On this basis, disparities between divergences estimated from molecular and organismal data may be interpreted as reflections of the erratic pace of organismal evolution. Finally, it is suggested that the biological significance of distinctions between populations is to be seen in the summation of the organismal and molecular data.

Key words: stock concept, organismal, molecular, evolution

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Dans la revue qui suit, nous présentons brièvement des arguments à l'appui de la thèse que l'évolution moléculaire procède à un taux régulier. Nous démontrons que cette thèse du taux régulier d'évolution des protéines structurales, connue sous le nom d'hypothèse du chronomètre moléculaire, s'applique aux genres de protéines dont on étudie communément la variation par des méthodes électrophorétiques et immunologiques dans des recherches sur la structure des stocks d'une population. Le sujet de la présente revue a été élargi pour démontrer, à l'aide d'exemples tirés de publications ichtyologiques, que le taux d'évolution organismique est plutôt erratique par comparaison avec celui de l'évolution moléculaire. Nous offrons une solution au paradoxe apparent du désaccouplement de l'évolution moléculaire et organismique fondé sur la suggestion publié par Allan C. Wilson et ses collaborateurs à l'effet que la divergence moléculaire entre n'importe quelle paire de populations devrait être considérée comme représentative d'une échelle temporelle pour cette divergence. Sur cette base, les disparités entre divergences estimées à partir de données moléculaires et organismiques peuvent être interprétées comme reflétant le taux erratique de l'évolution organismique. Enfin, nous suggérons qu'il faudrait percevoir la signification biologiques des différences entre populations dans la sommation des données organismiques et moléculaires.

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The most important thing to appreciate about the relationship between molecular and organismal evolution is that there generally is none.

Sarich 1977b

MANY investigations have shown that there is only a very tenuous correspondence between the rates of organismal and molecular evolution. In the present context organismal evolution (Wilson 1975) refers to the integration of the whole range of taxonomic characteristics such as morphology, ecology, behavior, etc. that determine and define the phenotype of an organism or species. Molecular evolution, for the purposes of this discussion, is restricted to the evolution of structural proteins, in which variation may be assessed by biochemical and immunological techniques. In some groups or organisms, molecular divergence is accompanied by organismal conservatism whereas in other groups of organisms the opposite seems to be true and we find organismal diversity accompanied by molecular conservatism. The issue which seems to be most important to the

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systematist or population geneticist is simply, what is the significance of the organismal and molecular data bearing on the specific stock identification question at hand?

To clarify this issue of the significance of the available data it will be necessary to review the basis of the evolutionary clock hypothesis as it relates to molecular evolution. This brief review will show that the molecular clock does not conflict with traditional views of the nature of organismal evolution; on the contrary the molecular clock will be seen to provide an independent confirmation of the view that the pace of organismal evolution is characterized by irregularity. Once these principles are established, examples from our own work and that of others will be used to illustrate the application of molecular and phenotypic data in the characterization of fish stocks.

The Steady Pace of Molecular Evolution

The lower vertebrates in general and the fishes in particular seem to have provided some of the more extreme examples of the lack of correspondence between organismal and molecular evolution. For this reason it seems necessary once again to restate the evidence for the regularity of the rate of molecular evolution, that is, the molecular clock, even though this and many other aspects of molecular evolution have been reviewed comprehensively by Wilson et al. (1977a). As well, other reviews of molecular evolution, and the relationship of molecular evolution to other aspects of evolution have been presented recently (Sarich 1977a; Ayala 1978; Kimura 1979). A detailed and lucid review of the biochemical and immunological techniques that are used in the acquisition of molecular data for systematic purposes has been presented by Bush and Kitto (1978).

The molecular approach to the study of evolution apparently has reached its zenith in respect to certain microorganisms where the total nucleotide sequence of the genome has been determined (Sanger et al. 1977). Although sequences of amino acids in proteins and nucleotides in genes represent the ultimate kind of molecular genetic information, the determination of these sequences remains a difficult and complex task which is beyond the resources of most students of systematics. The sources of molecular information that most systematic studies rely upon continue to be derived from electrophoretic studies of enzymes and immunological studies of various proteins (Sarich 1970; Sarich and Cronin 1976).

Evidence for a regularity in the rate of change of a biochemical characteristic that has come to be known as the molecular clock was first presented by Sarich and Wilson (1966). In this case the actual data were immunological relationships among primate albumins and it was shown, for example, that the immunological similarity (or difference) between human albumin and albumins of other primates was the same over large groups of these other primates. Thus, although there were differences in the relatedness of human albumin to albumins of other Hominoidea (apes, including chimpanzee, gorilla, organgutan, gibbon, and siamang), there was little difference in the relationship of human albumin to individual monkey species within the Cercopithecoidea (Old World monkeys). Similarly the immunological relationship of human albumin to several species in the Ceboidea (New World monkeys) and Prosimii (Prosimians) was, with one exception among the New World monkeys, constant within each group and within the limits of the technique. Similar data sets which included many reciprocal tests among primate serum albumins (Sarich and Wilson 1967a, 1967b) served to reinforce the observation that there is one average measure for the immunological relatedness of albumins between major groups of primates. What this means is that if one assumes that there was at some time in the past only one ancestor to both Hominoidea (man and the great apes) and Cercopithecoidea (Old World monkeys), then, since the time of the origin of these two divergent groups from their common ancestor, the amount of evolution of serum albumin has been constant in all the lineages comprising the two groups. If, during this time period, which is constant for the divergences of all the lineages from their common ancestor, the amount of albumin evolution has been reasonably constant in all the lineages, it surely follows that the rate of albumin evolution has also been constant within a reasonable degree of error. Another example of the same phenomenon regarding the evolution of serum albumin in the carnivores has also been presented by Sarich (1969). In this example, again, if it is assumed that the major groups of carnivores are monophyletic with respect to one another, then it becomes apparent that the evolution of serum albumin in the carnivores has also proceeded at a steady rate. These data thus show that, for serum albumin at least, there is a remarkable constancy in its rate of evolution. It is important to bear in mind that this conclusion is reached only by examination of the data itself and by the invoking of a single assumption, that certain groups or organisms are monophyletic in origin with respect to other groups.

It should be clear from the foregoing, as has been emphasized by Carlson et al. (1978), that the notion of a molecular clock is an internally consistent hypothesis that is quite independent of any correlations with dates inferred from paleontological data. On the other hand it is also possible to calibrate a molecular clock by reference to the fossil record and Carlson et al. (1978) present a method for this calibration.

In addition to these mammalian data regarding the constancy of serum albumin evolution in primates and carnivores, further immunological studies of other proteins as well as serum albumin have shown that the molecular clock hypothesis seems to hold in such diverse groups of organisms as insects (Beverley 1979), frogs (Maxson and Wilson 1975; Wallace et al. 1973), reptiles (Gorman et al. 1971), and birds (Prager et al. 1976; Prager and Wilson 1976; Ho et al. 1976). In all these examples the constancy of the rate of protein evolution appears as a simple empirical observation within reasonable statistical limits if one makes the conservative assumption that related groups of organisms are monophyletic with respect to one another.

For systematic purposes the immunological method of choice is the microcomplement fixation technique (Champion et al. 1974 and references therein). The relationship between two proteins is expressed as immunological distance (ID) (Champion et al. 1974; Sarich 1969). It has also been shown that when molecular clocks have been calibrated, ID is linearly related to the time of divergence of the lineages under consideration (Carlson et al. 1978). Furthermore, it has been shown for a number of proteins (Champion et al. 1974, 1975; Jollès et al. 1976) that there is a strong correlation ($r = 0.92$

in the latter work) between amino acid sequence differences and ID. Thus it is clear that there are various molecular clocks that move at constant rates, and in the clocks that are based on microcomplement fixation data we can be reasonably confident that ID estimates are an accurate reflection of accumulated amino acid sequence differences. Since amino acid sequence differences reflect mutational changes in structural genes, it follows that ID data also reflect mutational changes in structural genes. The steady rate of change of IDs thus implies a steady rate of fixation of mutations in structural genes.

Homologous proteins tend to evolve at the same rate regardless of the organism in which the protein is found (Sarich 1969), but there appear to be large differences in the rates of evolution of different classes of proteins (Nolan et al. 1975; Prager and Wilson 1976; Sarich 1977a; Wilson et al. 1977a). This is important to the immunological methods only insofar as data from two or more proteins may be complementary (Prager and Wilson 1976; Sarich and Cronin 1976), or the use of different proteins may allow for the estimation of a wider range of phyletic relationships (Gorman et al. 1971).

Despite the extensive application of this quantitative immunological method to the study of the evolution of a wide range of organisms, there seems to be no parallel example of the investigation of systematics among the fishes. The only exception seems to be some of our own work (J. W. Clayton and G. S. Bailey, unpublished observations) based upon the immunological similarity of heart-type lactate dehydrogenase (LDH H) among fishes in the order Salmoniformes. These data show that the salmon, trout, and Arctic grayling (*Thymallus arcticus*) are, as expected, closely related in terms of LDH H ID, but that some of the other fishes commonly classified in the order Salmoniformes apparently are very distantly related indeed, to the genera *Oncorhynchus*, *Salmo*, *Salvelinus*, and *Thymallus*. For fishes, the favored biochemical method for investigation of systematics, evolution, population genetics, and stock structure has been electrophoresis of proteins. It is thus both relevant and important to examine the electrophoretic data to see if it too seems to reflect the existence of a molecular clock or clocks.

The investigation of population genetics or systematic questions by electrophoresis generates arrays of population allele frequencies. These data have been analyzed by various means but the most generally applicable method at present seems to be that derived by Nei (1972) from theoretical considerations, whereby population genetic data of any number of genes and populations can be reduced to a set of genetic similarity (I) or genetic distance (D) values between every population pair in the group. The original method has been refined by Nei (1978) to take into account more thoroughly the effects of the sample sizes of both genes and genomes. The general conclusion that the number of genes is more important than the number of genomes in the distinction of populations was also reached by Gorman and Renzi (1979) in an empirical study.

The fundamental question remains, however, do D values vary in a regular way; that is, do these parameters based on allelic frequency differences also constitute another example of the molecular clock? This question has been addressed indirectly through tests of the relation between D and albumin ID for series of species pairs (Case et al. 1975; Sarich 1977a; Maxson and Maxson 1979; Wyles and Gorman 1980). The rationale for these indirect tests stems from the many empirical observations that albumin ID measurements represent a molecular clock and therefore if D is strongly correlated with albumin ID then D too must represent a molecular clock. This approach has the advantages that many data sets can be compared on a common basis and the comparison can be analyzed for statistical significance (Sarich 1977a).

The extensive body of data drawn from many sources and presented by Sarich (1977a) shows, among a total of 76 species pairs, that there exists a strong correlation ($r = 0.82$) between the electrophoretic D and albumin ID. In one respect, this high correlation seems surprising because, as we have seen (Nolan et al. 1975; Prager and Wilson 1976; Wilson et al. 1977a), different proteins each tend to evolve at unique rates. One might therefore anticipate that Nei genetic distance estimates would be very dependent upon the choice of proteins for electrophoretic analysis. Sarich (1977a) has emphasized this point and suggested ways to consider the variable rates of evolution of proteins to calibrate an electrophoretic distance molecular clock. If these variable rates of evolution are considered, it seems clear that Nei D values do represent a molecular clock.

More detailed analyses of the relation between D and albumin ID in individual data sets (Maxson and Maxson 1979; Wyles and Gorman 1980) demonstrated considerable variation both in the strength of the correlation as shown by a range in r from 0.361 to 0.829 and also in the slope of the ID versus D plot. While some of the variation seems to be due to vagaries of the electrophoretic data, the analysis of Maxson and Maxson (1979) also revealed a 'saturation' effect which occurs in D estimates for $D > 1.0$. It seems clear from this analysis that while D values may satisfactorily represent a molecular clock in the range $0 < D < 1.0$, at higher D values there are a number of complications (Maxson and Maxson 1979) that frequently cause D to be an underestimate of the true molecular divergence. The Nei D thus should represent a molecular clock for low D values such as are commonly found between stocks within species and between species within many genera, although in comparisons between higher taxa, it may not be reliable as an estimator of molecular divergence.

Organismal Evolution Versus Molecular Evolution

The regularity which we see in the rate of evolution of the structural genes of proteins seems in some ways to reflect the gradualism in organismal evolution that was favored by Darwin. However, modern interpretations of the fossil record have strongly emphasized the erratic pace of organismal evolution (Eldredge and Gould 1972; Ager 1973; Gould 1977a, b; Gould and Eldredge 1977; Stanley 1979; Vrba 1980). Among living forms some of the best known examples of the independence of the rates of organismal and protein evolution come from comparative studies of frogs and mammals (Wallace et al. 1971, 1973). These investigations show that frogs, although morphologically very conservative, have experienced rates of serum albumin evolution that are comparable to the rates observed in mammals. It would seem that the significance of these kinds of investigations can be seen

best in light of the hypothesis put forward by Wilson et al. (1977b). These authors suggested "that sequence evolution is primarily a function of time and proceeds as rapidly in phenotypically conservative creatures as in those which have changed radically in phenotype." In other words, we may take the molecular data as representative of a time scale against which it should be possible to determine whether a given population assemblage is experiencing fast or slow organismal evolution.

Among the fishes, the situation is complex, because while fishes represent an ancient group of organisms, they also represent many rather recent species radiations and furthermore they also represent, with regard to organismal evolution, examples of both conservatism and relatively rapid change. Turner (1974) described a group of relict pupfish (*Cyprinodon*) species from the Death Valley area of California. Evidently they have become isolated in various disjunct habitats only within the last million years or less and the biochemical data indeed show that there has been little molecular divergence among these species. On the other hand, the morphology and ecological preferences indicate that these species are highly divergent in many respects. Further examples of a similar situation seem to have been observed in investigations of some Mexican cichlids (*Cichlasoma*) (Kornfield and Koehn 1975; Sage and Selander 1975). In both studies the widely distributed Rio Grande cichlid (*Cichlasoma cyanoguttatum*), and two closely related forms that are found in a very restricted area (the Cuatro Cienegas Basin) were examined biochemically, and also a variety of morphological and ecological factors were considered. The organismal data clearly show that there are two forms endemic to the Cuatro Cienegas Basin while the biochemical data show that these two forms are virtually identical and only slightly different from the wide-ranging *C. cyanoguttatum*. Kornfield and Koehn (1975) seem to favor the explanation that speciation has occurred in the Cuatro Cienegas cichlids without "random genetic reorganization." Sage and Selander (1975) favor a different explanation in which the two forms are considered to be simply alternate genetic morphs of a single species. While final resolution of this question would seem to require more information regarding the extent of reproductive isolation that actually exists between the forms (see for example McKaye and McKaye 1977), a viable alternate explanation would appear to be that this is just another example of rapid organismal divergence. From this point of view the high degree of protein similarity is simply another way of saying the organismal divergence has been extremely rapid; that is, it has occurred in a period of time too short to have allowed the accumulation of significant protein changes. A further example of rapid organismal evolution in the presence of very little structural protein divergence was reported in African cichlids (Kornfield 1978). In another similar investigation, Loudenslager and Kitchin (1979) found two forms of cutthroat trout (*Salmo clarki*) that were readily distinguished by organismal features although they were almost identical according to the biochemical characters that were examined.

In contrast to these observations of apparently rapid phenotypic evolution in fishes, other investigations have found the opposite situation whereby the biochemical data seem to reveal cryptic species that are phenotypically identical, or nearly so. Thus, Shaklee and Tamaru (1977) found that in bonefish (*Abula vulpes*) a very modest degree of morphological divergence occurred concomitantly with a Nei genetic distance of 1.3. In fishes (*Abudefduf*, Pomacentridae) now separated by the Panamanian Isthmus, Gorman and Kim (1977) found two nominal species that are difficult to distinguish morphologically although they are characterized by a genetic distance of 0.32. These authors further suggest that this genetic distance indicates a time of genetic isolation of about 5 million years, a time in accord with the estimated age of the Panamanian Isthmus.

There are of course other situations where the biochemical divergence seems either to match the organismal divergence or to produce a phylogeny that is similar to the classical phylogeny based upon phenotypic characters. Thus, in a biochemical investigation of sunfishes (Centrarchidae) Avise et al. (1977) were able to demonstrate that a phylogeny based on biochemical genetic similarity comparisons among the species agreed very well with a phylogeny based on morphological characters. Similarly, a phylogeny of cichlid fishes (Cichlidae) from the Sea of Galilee derived from biochemical data was also found to parallel the classical phylogeny (Kornfield et al. 1979). An investigation of several Pacific salmon species (*Oncorhynchus* sp.), cutthroat trout, and rainbow trout (*Salmo gairdneri*) showed that a phylogeny derived from biochemical data was in substantial agreement with phylogenies derived from morphological and ecological data (Utter et al. 1973 and references therein). It seems reasonable to conclude that while there are some examples of roughly equivalent rates of morphological and biochemical evolution, there are too many examples of nonequivalence of these rates to allow one to assume that these two kinds of evolution are likely to be occurring at the same rate in any given situation.

The regularity we see in the evolution of the structural genes of proteins seems to be in almost paradoxical contrast to the erratic rate of organismal evolution. Apparently the important question is not so much how can this paradox be resolved, but rather what is the significance of these two very different kinds of evolution that seem to be going on simultaneously in all manner of organisms. For the purposes of this symposium, this question should evidently be restricted to an inquiry into what is the significance of these two kinds of evolution to investigations of population genetics and stock structure.

If we accept the suggestion of Wilson et al. (1977b) that the divergence of structural gene loci (which is in effect the kind of divergence that electrophoresis and microcomplement fixation measure in the present context) represents a time scale, then we should see that the significance of the probable difference between the rates of molecular and organismal evolution in a particular investigation is determined by the question addressed in that investigation. Thus, among pairs of populations, molecular data alone will probably be sufficient to determine whether reproductive isolation has been achieved or to estimate the relative time since divergence. If, however, we want to know if the stocks are sufficiently different in the phenotypic sense that they will not completely merge given the opportunity, then probably more data relating to the organismal divergence will be required. The opposite kind of question, namely if a stock is lost, is it likely to be replaced or replaceable from other similar stocks is also of obvious interest in fisheries. Again I would suggest that a combination

of molecular and organismal data is much more likely to produce useful answers than is either kind of data used alone. I will try to illustrate this with some examples from our own and other work.

Organismal and Biochemical Data In the Discrimination of Fish Stocks

The lake whitefish (*Coregonus clupeaformis*) population in Squanga Lake, Yukon Territory has been shown to represent two divergent forms (Lindsey 1963). These forms are distinguished by a number of morphological and ecological factors, and furthermore the existence of similar sympatric forms has been observed in three other Yukon lakes, one of which is ~200 km distant from Squanga Lake on a completely different drainage system (Bodaly 1977, 1979). Our biochemical data regarding many lake whitefish populations from central and northwestern North America have revealed a marked discontinuity in the frequencies of many isozyme alleles, as well as in the phenotypes of hemoglobin and some other isozyme systems of incompletely understood genetic nature (Lindsey et al. 1970; Franzin and Clayton 1977). The geographic location of this major discontinuity in the distribution of biochemical characters is roughly coincident with limits of range expansion, that can be inferred from available geological data (reviewed by Foote 1980; Franzin 1974), for lake whitefish stocks emigrating from the Bering and Mississippi–Missouri glacial refuges at the close of the Wisconsin glacial period. More recent investigation of lake whitefish populations in the boundary zone has produced further evidence of the discontinuity of isozyme alleles and phenotypes that is consistent with a third suite of lake whitefish populations in northwestern North America that could be interpreted as evidence for survival, isolation, and biochemical divergence of lake whitefish in a Nahanni glacial refuge (Foote 1980). Geological evidence for the possible existence of a Nahanni glacial refuge has been presented by Ford (1976). In marked contrast to the molecular data which show considerable divergence between lake whitefish stocks that were probably also separated in the past by one or more glacial episodes, all the populations within the Yukon Territory including the sympatric, morphologically, and ecologically divergent forms show considerable biochemical uniformity (Bodaly 1977).

The key insight into explaining these observations seems to be found in the suggestion of Wilson et al. (1977b) that the biochemical data should be interpreted as providing the time base against which the organismal data may be interpreted. We would thus suggest that lake whitefish of the Yukon Territory (and probably also Alaska and waters in British Columbia tributary to the Yukon River) have been isolated from central North American lake whitefish for a long period of time. At some time subsequent to the beginning of this period of isolation of what we may call the Bering refuge stock, it seems that an organismal divergence began within the Bering refuge stock. Evidently this organismal divergence has led to the stocks we see today in Squanga, Little Teslin, Teenah, and Dezadeash lakes (Bodaly 1979). The very slight biochemical distinction between the Squanga, etc., sympatric forms should not be seen as posing a question as to the significance of the organismal data, rather it should be seen as merely dating the organismal divergence as relatively recent. That there are apparently no morphological correlates to the relatively marked biochemical differences between Bering and non-Bering refuge derived lake whitfish may be due more to the notorious tendency among coregonid fishes to exhibit continuous gradations of morphological and meristic characters than to the real absence of significant organismal differences between Bering and non-Bering refuge derived lake whitefish. Even this statement must be qualified because, as McPhail and Lindsey (1970) have noted, lake whitefish from much of Alaska have the lowest gill-raker counts among all North American lake whitefish, and these authors regard gill-raker count as one of the most reliable of characters for distinguishing lake whitefish populations. It is of course gill-raker number which is one of the major characters that distinguishes the two forms of lake whitefish in the Yukon lakes (Lindsey 1963; Bodaly 1977, 1979). Also, there are other lake whitefish populations in North America that are distinguished by bimodal counts of gill-raker number (Lindsey et al. 1970). One of these unusual lake whitefish population groups from Maine has recently been studied biochemically (Kirkpatrick and Selander 1979). These authors made morphological distinctions on the basis of dwarfism, which Fenderson (1964) showed to be somewhat more reliable than high gill-raker number in the identification of the unusual member of these sympatric pairs of lake whitefish. In both reports (Fenderson 1964; Kirkpatrick and Selander 1979) the dwarf form was characterized by earlier maturity at a much smaller size than the other more normal morphological form. The biochemical differences among the various normal and dwarf forms were all very small but Kirkpatrick and Selander (1979) concluded that the dwarfs and normals do represent independent gene pools. Our own biochemical data (Lindsey et al. 1970, R. A. Bodaly, J. W. Clayton and C. C. Lindsey, unpublished observations) strongly suggest that the sympatric divergent forms from Maine arose independently from those in the Yukon.

Among other salmonids, sympatric, organismal divergence with dwarfing of one of the forms has been observed in kokanee (*Oncorhynchus nerka Kennerlyi*) in Kamchatka (Kurenkov 1977) and also in brown trout (*Salmo trutta*) in Sweden (Ryman et al. 1979). In the former study of kokanee no biochemical data were presented, but the phenotypic data show convincingly that there are two forms with many similarities to the two lake whitefish forms found in Squanga Lake (Lindsey 1963). In contrast, Ryman et al. (1979) presented an extensive set of biochemical data regarding the sympatric brown trout forms. The authors concluded that although the biochemical data were consistent with reproductive isolation of these stocks, there was, in total, remarkably little biochemical genetic divergence between them.

The marked organismal divergence evident in these examples is seldom encountered in the management of fisheries. In most fisheries there seems to be a more or less continuous gradation of morphological and ecological characteristics among the fish stocks. This continuous gradation of organismal characters coupled with their uncertain genetic basis has caused some fishery biologists to turn toward biochemical methods as a means to sort out the stock structure in various fisheries. It would seem that such investigations will

have a greater likelihood of producing meaningful results if all the available opportunities for the detection of both organismal and biochemical divergence are utilized. An example of this kind of study is provided by Kristofferson (1978), who investigated the population structure of lake whitefish in Lake Winnipeg. The fish examined in this study were collected at times and locations at or near which most of these lake whitefish spawn. It was thought that this would maximize the chances of detecting subpopulations since if there were reproductively isolated stocks they should be separated at spawning time although they might not be separated at other times. The results of the combined biochemical and morphological investigation showed that one stock could be distinguished from all the others by both biochemical and morphological characters (Kristofferson 1978). Of the remaining stocks, which were uniform according to the limited suite of biochemical characters which were used, four groups could be resolved on the basis of morphological differences.

These examples seem to point to the conclusion that the delineation of fish stocks will, in most cases, require the combined data of both biochemical and classical biological study. If only one kind of data is used, the interpretation would appear to be much less reliable. This is not to say that there are not special situations in which only one kind of data will suffice. Thus, anadromous and non-anadromous Arctic char (*Salvelinus alpinus*) have been distinguished strictly on the basis of their morphology and meristics (Blouw 1977). On the other hand a single isozyme difference clearly distinguishes the morphologically similar walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) (Clayton et al. 1973). This latter principle was recently used in a study of the sauger of Lake Winnipeg, whereby it was shown that very large sauger from a lightly exploited stock were in fact sauger and not walleye–sauger hybrids as might have been expected from the large size of the fish (Lysack and Ebbeling 1980). It seems inescapable that the methods used will have to be selected on the basis of the fish stock question that is being addressed.

Is There a Molecular Correlate of Organismal Evolution?

Up to this point the only kind of molecular data that has been considered relates to similarities and differences among structural proteins. In practice this is the information that is obtained by either immunology or protein electrophoresis. As we have seen, these data show that structural proteins and thus the genes that code for these proteins change at rather steady rates with respect to time. It has been known therefore, from the time that these molecular clocks were discovered, that they could not be directly related to the organismal evolution of the creatures in which they are found. This situation, while it does not, as I hope I have shown, inhibit our use of the data (a point made most eloquently by Sarich 1977b), it still leaves open the question as to what might be the molecular correlate of organismal evolution. It has been suggested that evolutionary changes in both the organization of structural genes and in the genes that regulate development may play a very important role in adaptive, organismal evolution, and considerable evidence has been presented on this point (Wilson et al. 1974a, b; Wilson 1975; Prager and Wilson 1976; McDonald and Ayala 1978). It would be inappropriate to attempt discussion of this topic in this symposium because the kinds of data which have been used to support arguments that evolution of gene regulation and/or gene arrangement is correlated to organismal evolution do not lend themselves to the investigation of either general questions of population genetics or questions of fish stock structure.

Summary and Conclusion

One could not conclude a discussion such as this without making a final reference to the brilliant essay by Sarich (1977a) regarding the molecular approach to evolutionary studies. Among the major points which Sarich (1977a) emphasizes, those of particular relevance to fish stock discrimination seem to be the disparate rates of evolution of specific proteins and the selection of appropriate molecular measures for the particular evolutionary divergence one is seeking to understand. Thus, although the enzymes that are often assessed electrophoretically represent a class of relatively slowly evolving proteins, gene frequency measures among these enzymes are probably the best data we have for estimating very recent divergences among populations of a species. This has to be qualified, however, by the actual choice of proteins in any particular study. Thus it should be clear that since different proteins evolve at different rates, genetic distance estimates between studies that utilize different suites of proteins will have to be compared with caution and close regard for the actual data base. For slightly greater evolutionary distances between closely related species, Sarich (1977a) recommends a simple electrophoretic band counting procedure. This method would seem to have some application in fishery studies and it probably deserves more attention than it has received. For moderate evolutionary distances the microcomplement fixation procedure clearly seems to be the method of choice. Probably many of the higher-order fish taxonomies could be very profitably investigated by this method. Similar conclusions regarding the application of biochemical methods appropriate to the phylogenetic divergence under consideration were also proposed by Bush and Kitto (1978). If, as it seems, electrophoretic gene frequencies are likely to continue to be the main biochemical input into fish stock investigations, then I suggest that these data should be made as reliable as possible by firstly paying close attention to the actual genetics of the systems utilized, and secondly to use the very best electrophoretic methods that can be devised to come as close as possible to extracting all of the genetic information from the proteins. On this latter point there have been a number of publications in which various kinds of "hidden" electrophoretic variation, that is, hidden by inadequate or incomplete technique, have been revealed by more adequate methodology (Stenzel and Brimhall 1977; Johnson 1977 and references therein). It has in fact been shown recently that almost every kind of amino acid substitution can be detected by an adequate electrophoretic procedure (Ramshaw et al. 1979).

While the preceding comments should indicate the way towards an adequate and appropriate molecular data set, we may anticipate many questions of fish stock discrimination which cannot be resolved by molecular data alone. In such

investigations it will probably be necessary to combine the molecular data with morphological, ecological, and behavioral data to approach the biological significance of the fish stocks in question. In the interpretation of the summation of the combined molecular and organismal data, the use of the molecular data as a time base (Wilson et al. 1977b) seems to have a great deal of merit.

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The Stock Concept from the Viewpoint of Population Genetics[1]

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ALTUKHOV, YU. P. 1981. The stock concept from the viewpoint of population genetics. Can. J. Fish. Aquat. Sci. 38: 1523–1538.

Results are presented of a comparative study of the spatial and temporal structure of fish species from the standpoint of biochemical population genetics. Local fish stocks within historically established natural boundaries are considered as genetically stable population systems, in contrast to the elementary populations, which are variable structural components of such systems. The general principle in maintaining a rational fish industry is formulated on the basis of an approach to the population system as a whole, to distribute the appropriate efforts among all components of its structure.

Key words: biochemical population genetics, stock concept of fish, optimal fishing industry

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On trouvera dans l'article qui suit les résultats d'une étude comparative de la structure, dans le temps et dans l'espace, d'espèces de poissons sous l'angle de la génétique biochimique des populations. Dans des limites naturelles établies depuis longtemps, les stocks locaux sont considérés comme systèmes de populations stables, contrairement aux populations simples, qui sont des éléments structuraux variables de tels systèmes. Le système de populations, dans l'ensemble, est à la base de la formulation du principe du maintien d'une industrie halieutique rationnelle — soit la répartition d'efforts appropriés parmi tous les éléments de la structure.

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IN planning a complex of measures to preserve the biosphere, not only the prevention of its direct destruction should be borne in mind, but also the prevention of external influences with remote deleterious effects. Of particular importance is the exploitation of economically valuable species without due regard for the specific features of their inner structure — their subdivision into more or less isolated, hereditarily different groups, i.e. populations.

All biologically important characteristics of populations, including their size and productive efficiency, are determined by the historically established gene pools. Therefore, the population-genetic analysis of species in nature is of primary importance in developing an optimal strategy for their efficient management. If this strategy is to provide not only for maximum economic benefits but also for continuous maintenance of natural populations, we must emphasize the importance of elucidating the factors and conditions that permit populations and species to do so.

The purpose of this communication is to look at the problem of so-called local fish stocks from this viewpoint, and to characterize these populations as the basic objects of genetic research and management.

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Factors and Conditions of Genetic Stability of Populations

PRINCIPLES OF THE APPROACH

Population genetics studies the natural patterns of the preservation and evolution of the genotypic structure of populations in time and space. The theoretical basis is the Castle–Hardy–Weinberg law describing the fate of genetic information in a panmictic population of indefinitely large size and having no environment: in such an unstructured community, the proportions of genotypes, and therefore of gene frequencies, achieve the point of stable equilibrium in the first generation after random mating, and remain constant throughout an indefinitely long series of generations.

But such ideal populations do not actually occur in nature because there are factors that shift them from the equilibrium point and disturb their stability, leading to change in their genetic structure. One such factor is natural selection, which can result in the production of a larger number of progeny by some genotypes than by others. Other factors are mutation and migration of genes. Finally, random genetic drift may occur, in which case, because of limited size, the population "makes an error" when transferring genes to the next generation.

If all these factors influence a population simultaneously, its internal structure will become more complex. A panmictic population may then split into several more or less interrelated subpopulations. The distribution of gene frequencies in such

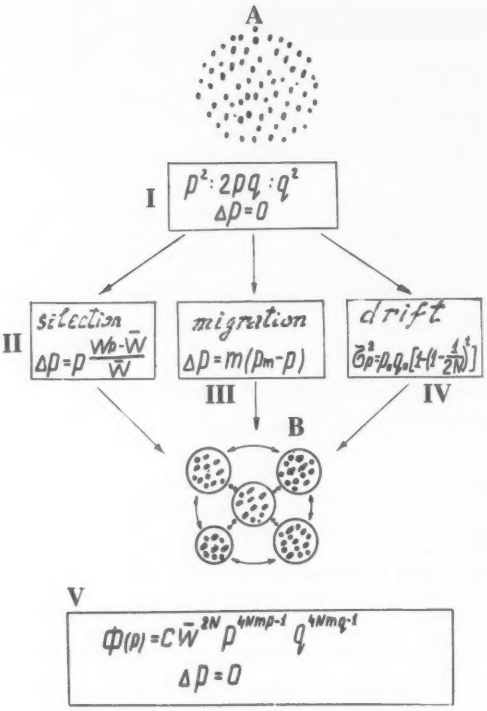

FIG. 1. Basic mathematical models of population genetics. A, an infinitely large panmictic population remaining stable ($\Delta p = 0$) in the absence of selection (W), migration (m), and genetic drift (N), according to the Castle–Hardy–Weinberg law expressed by formula I, where p and q are gene frequencies combined randomly in homozygous (p^2 and q^2) and heterozygous (pq) genotypes; II, III, IV, elementary formulae for selection, migration, and genetic drift, respectively, as main factors responsible for changes in gene frequencies (Δp). B, a subdivided population formed under the simultaneous action on its genetic structure of selection, migration, and genetic drift; V, mathematical formula for gene frequency distribution in such a population.

a subdivided population will become stable and stationary again because of an equilibrium established between centrifugal and centripetal tendencies. These are the so-called "microevolutionary" processes, which are described in a very general way in population genetics theory by the formulae shown in Fig. 1.

The basic mathematical models in population genetics were elaborated in the 1930s (Fisher 1930; Wright 1931; Dubinin 1931; Haldane 1932; Dubinin and Romashov 1933). However, their practical application requires that at least two main conditions exist. Firstly, it is genes that should be analyzed as elementary hereditary units, and secondly, gene distribution should be studied in populations that have been fully characterized as integral biological units.

Although these requirements appear simple, they are not as easy to satisfy as it might appear.

Although gene frequency is the basic population-genetic parameter, it can characterize a population only when the gene in question has a marked phenotypic effect. For instance, if a feature of animal coloration is controlled by several alleles at a particular gene locus, this results in the existence of several hereditary morphs. This type of variation is called genetic polymorphism and can be easily studied. But many species do not display polymorphism and are uniform in appearance, their genes are unobservable, and a direct population-genetic analysis is impossible. Because of this, until recently, investigation of the genetics of natural populations has been limited to a few species that are polymorphic in external appearance. Only during the last decade, because of the progress of immunological and biochemical genetics, have important changes occurred: in many species allele gene systems have been detected coding for synthesis of blood groups and different proteins of an enzymal or nonenzymal nature. This "hidden" hereditary variation is revealed either by immunological reactions or by electrophoretic methods. Figure 2 illustrates schematically electrophoretic hereditary variants of different proteins described for Pacific salmon by American, Soviet, and Japanese researchers (see: Altukhov 1974; Allendorf and Utter 1978), using protein electrophoresis in starch and acrylamide gels. The discovery of wide biochemical hereditary variability in natural populations has opened new possibilities for their comparative investigation. Nowadays, this research area is fundamental in population genetics (Lewontin 1974; Altukhov 1974; Nei 1975; Ayala 1976; Allendorf and Utter 1978; Nevo 1978; Kirpichnikov 1979).

The other important condition for progress in this field concerns the choice of research objects. Any branch of biology has its own objects, whether molecules, cells, or individuals. There are no disagreements, in fact, among cytologists, anatomists, and molecular biologists as to the reality and entity of the levels they study. But turning to ecology or population genetics, we can see no such unity: it is possible to cite more than a dozen names used to designate intraspecific animal and plant communities — "population," "Mendelian population," "deme," "ecotype," "morph," "elementary population," "microtopographic race," "stock," "parcella," etc.

A universal, unambiguous terminology is an indication of the maturity of any branch of science. Clearly, this cannot be said in regard to population biology, which is still at the analytical stage of development, reflecting the individual interests of morphology, taxonomy, ecology, and other disciplines concerned with the population level of the organization of life. At the same time, it has become more and more evident that such terminological diversity reflects also certain fundamental features that exist at the population level, but which are often disregarded. The most important is the complexity that is determined by intrinsic principles of hierarchic structure. Only when this complexity is taken into account does a comparative population-genetic study become possible. Further, we shall present the principal results using this approach with isolated natural populations of fish — i.e. so-called local stocks isolated from each other by natural boundaries, that is, any historically established barriers that determine certain mosaics of spatial distribution of a species over its range.

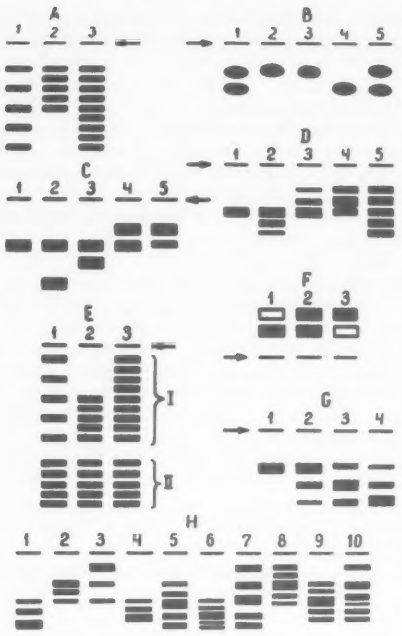

FIG. 2. Hereditary electrophoretic protein variants in Pacific salmon. A, blood serum Ldh: 1, 2 — BB and B′B′ homozygotes, respectively; 3 — B′B heterozygote. B, sockeye muscle phosphoglucomutase: 2, 3, and 4 — BB and AA homozygotes respectively; 1, 5 — AB heterozygotes. C, chum serum albumin phenotypes: 1 — C, 2 — AC, 3 — BC, 4 — CD, 5 — D. D, chum muscle malate dehydrogenase phenotypes: 1 — A phenotype; 2 — B, 3 — C,4 — C′,5, — D.F, chum blood serum Ldh phenotypes: 1 — F, 2 — FS, 3 — S. E, chum muscle Ldh genotypes: 1 and 2 — AA and A′A′ homozygotes, respectively; 3 — A′A heterozygote. G, chum liver AAT genotypes: 1 — AAAA, 2 — AAAA′, 3 — AAA′A′, 4 — AA′A′A′. H, chum liver isocitrate dehydrogenase genotypes: 1 — FF, 2 — SS, 3 — S′S′, 4 — F′F′, 5 — FS, 6 — FF′, 7 — FS, 8 — S′S′, 9 — F′S, 10 — FS′.

An important feature of our approach is that we have studied both self-reproducing native stocks that are not yet completely destroyed by a fishery (deepwater redfish *Sebastes mentella* in the Northwest Atlantic, anchovy *Engraulis encrasicholus* in the Black and Azov Seas, sockeye salmon *Oncorhynchus nerka* in one of its spawning lakes in Kamchatka) and artificially maintained populations (chum salmon, *Oncorhynchus keta*).

In addition, when studying these species (characterized by very different ecologies), we hoped to reveal both distinctive and common features of the genetic organization of their local stocks.

During the course of expeditions over the last 20 years, we have studied many thousands of fish for various gene markers (blood groups and proteins) and have discovered new facts that have justified the population-genetic approach to the problem of local stocks as the basic unit for management.

Local Fish Stocks as Reproductively Isolated, Genetically Heterogenic Populations

All populations compared revealed clear genetic differences, most often related to the gene frequencies in all of them, but sometimes to genes characteristic of a single population or group of populations. For example, the A_2 blood group gene, which occurs with an average frequency of 0.73 ± 0.01 in the Newfoundland redfish stock, is close to fixation in the Flemish-Cap region ($\bar{q} = 0.95 \pm 0.02$; range in samples from 0.91 to 1.00). The A_o blood group that occurs with high frequency in Azov anchovy is practically absent in the Black Sea race.

Such differences between local stocks — evidence of their reproductive isolation — proved to be stable in time: no noticeable interpopulational gene exchange was recorded in three generations of Azov anchovy or in several chum stocks, except for cases associated with the transportation of artificially fertilized eggs from one basin to another for the purpose of acclimatization (Altukhov 1974).

To illustrate this, consider the data on genetic differentiation of chum salmon stocks studied by our group from 1968 (Fig. 3). Tables 1 and 2 characterize the genetic features of the populations under study for a number of polymorphic protein loci. Both tables give the dates of the studies, the volume of material collected, and the gene frequencies at the lactate dehydrogenase (Ldh-A^2, Ldh-B^2), albumin (Alb), aspartate aminotransferase (AAT), and isocitrate dehydrogenase (s-Idh) loci, as well as the malate dehydrogenase (Mdh) phenotype frequencies. The spawning chum stocks in the Naiba and Kalininka rivers were thoroughly studied by us for 7–9 years; each year several samples taken throughout the spawning run were analyzed. Hence we present more detailed data for individual generations of these populations, as well as the results of a test for homogeneity of samples from one generation (Table 3).

The stocks of the Tym′, Kurilka, and Reidovaya rivers have been studied in less detail: the number of generations analyzed is smaller, and the samples represent only part of the spawning run. Single samples characterize the population whose spawning run passes through Lake Tunaicha to the Udarnitsa River; only one sample was taken from the Buyuklinka River, a tributary of the Poronai River. The autumn race of Amur chums, represented by samples from the Teplov population, was studied in detail during the spawning run, but only in one generation; for this population we present only summary data for the loci studied.

In Fig. 4, the populations studied are shown graphically following the data on the phenotype frequencies of a variety of protein systems (except for rare phenotypes). The highest geographical variation characterizes the allele frequencies at the s-Idh and Ldh-A^2 loci and the Mdh phenotype frequencies; the frequencies at the other loci vary less, although it is possible to find differences between the populations for almost any loci. Thus, the differences in the Ldh-A^2 allele frequencies are most pronounced between the Sakhalin, Kuril, and Amur populations; the Naiba River population is differentiated from practically all the other populations studied, including Japanese (Numachi et al. 1972) and American (Utter et al. 1973) populations, by a high frequency of occurrence of the heterozygous phenotype Mdh-B, which is absent

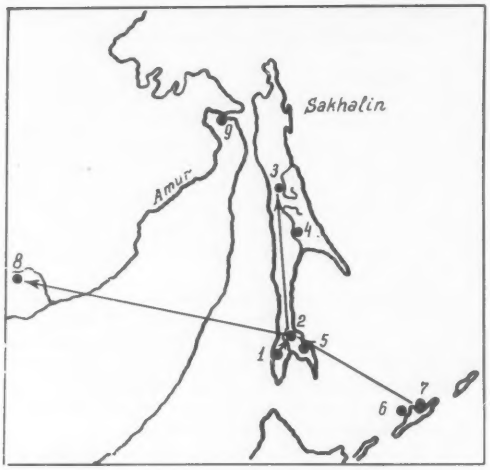

FIG. 3. Regions of population–genetic studies of chum salmon stocks during the reproductive period (in rivers). 1, Kalininka River; 2, Naiba River; 3, Tym′ River; 4, Poronai River; 6, Kurilka River; 7, Reidovaya River; 8, Lake Teploe (Amur River). Arrows indicate the direction of acclimatization transfers.

or rare in the other populations. A high frequency of another heterozygous phenotype, Mdh-C, is characteristic of the Kalininka River population, which has a specific genetic structure at most loci. This distinguishes it from the populations of eastern and southeastern Sakhalin and Iturup (one of the Kuril islands), which resemble each other. The similarities and differences between the populations are well shown in Fig. 4. The Tym′ River population occupies an intermediate position between the Naiba River and Kuril populations: it is closer to the Kuril population in respect to the Mdh-C phenotype frequency, and to the Naiba River population in respect to the Ldh-A^2 allele frequencies.

Thus, almost every one of the populations has its own characteristic genetic features, which (except for the Alb frequencies) persist from generation to generation.

On the whole, the Kalininka River population is more stable from year to year in its genetic features than is the Naiba River population. This is probably because the Naiba River population has been more influenced by various acclimatization measures.

Indeed, as pointed out earlier (Altukhov 1974), in 1969–71 when the abundance of chums in the Naiba River was high enough and chums were studied more completely throughout the spawning run, a mixture of chums from the Kalininka River could be observed. In 1964–71 large quantities of fertilized eggs from the Kalininka were transferred

TABLE 1. Allele frequencies at Ldh-A^2, Alb, Ldh-B^2, s-Idh, and AAT loci in chum populations (*N* represents number of fish studied; number in parentheses represents number of samples taken during spawning run).

Site (rivers) and time of collection of material	Ldh-A^2		Alb		Ldh-B^2		s-Idh					AAT	
	N	pA	*N*	pD	*N*	pF	*N*	pF	qS	rS′	sF′	*N*	pA
Naiba													
Oct. 1968	144 (2)	0.9514	—	—	115 (2)	0.878							
Oct.–Nov., 1969	641 (7)	0.961	506 (6)	0.318	291 (6)	0.850							
Sept.–Nov., 1970	101 (1)	0.931	522 (10)	0.672	478 (9)	0.838							
Oct.–Nov., 1971	276 (5)	0.962	257 (5)	0.714	277 (5)	0.861							
Oct., 1972	88 (2)	0.966	83 (2)	0.596	86 (2)	0.913							
Oct.–Nov., 1973	244 (5)	0.953	243 (5)	0.798	246 (5)	0.913							
Oct., 1975	194 (4)	0.941	190 (4)	0.650	200 (4)	0.900							
Oct., 1976	150 (3)	0.877	144 (3)	0.795	150 (3)	0.953	105 (3)	0.409	0.391	0.133	0.067	150 (3)	0.950
Oct., 1977	147 (3)	0.932	91 (2)	0.830	100 (2)	0.880	142 (3)	0.356	0.493	0.116	0.035	150 (3)	0.965
Sept.–Oct., 1978	200 (4)	0.935	193 (4)	0.718	147 (3)	0.908	194 (4)	0.461	0.405	0.070	0.065	198 (4)	0.951
Total	1285	0.9465	2229	0.624	2143	0.876	441	0.415	0.430	0.100	0.055	498	0.955
Kalininka													
Oct., 1969	146 (3)	0.969	—	—	80 (2)	0.894							
Sept.–Oct., 1970	—	—	352 (4)	0.872	401 (4)	0.859							
Sept.–Oct., 1971	161 (4)	0.985	176 (4)	0.883	145 (3)	0.883							

TABLE 1. (*Concluded*)

Site (rivers) and time of collection of material	Ldh-A²		Alb		Ldh-B²		s-Idh					AAT	
	N	pA	*N*	pD	*N*	pF	*N*	pF	qS	rS′	sF′	*N*	pA
Sept.–Oct., 1974	385 (4)	0.996	397 (4)	0.778	399	0.816							
Sept., 1975	100 (2)	1.000	47 (1)	0.830	100 (2)	0.695							
Sept.–Oct., 1976	125 (3)	1.000	125 (3)	0.868	125 (3)	0.744						125 (3)	0.918
Sept.–Oct., 1977	150 (3)	0.983	84 (2)	0.923	100 (2)	0.825	150 (3)	0.650	0.267	0.0800	0.003	149 (3)	0.908
Sept.–Oct., 1978	148 (3)	0.993	147 (3)	0.922	148 (2)	0.855	149 (3)	0.685	0.262	0.054	0.000	150 (3)	0.935
Total	1271	0.990	1328	0.852	1498	0.828	299	0.667	0.264	0.067	0.002	424	0.920
Tym′, total													
Sept.–Oct., 1969–73, 1976	514 (8)	0.946	380 (5)	0.763	592 (9)	0.908	—	—	—	—	—	54[a] (1)	0.954
Buyuklinka (Poronai tributary) Oct., 1976	88 (1)	0.955	—	—	—	—	86 (1)	0.517	0.343	0.046	0.064	88 (1)	0.926
Udarnitsa, total													
Oct., 1972, 1977, 1978	198 (4)	0.922	144 (3)	0.889	150 (3)	0.957	98 (2)	0.480	0.362	0.117	0.041	100 (2)	0.957
Kurilka, total													
Oct., 1970 1972, 1977, 1978	412 (7)	0.836	386 (6)	0.663	400 (6)	0.916	124 (2)	0.548	0.292	0.160	0.000	124 (2)	0.956
Reidovaya, total Oct., 1970–72	193 (3)	0.749	151 (3)	0.414	175 (3)	0.920							
Kurils, total	605	0.808	537	0.619	575	0.917							
Amur, Teploe Lake, total (autumn race) Sept.–Oct., 1974	412 (9)	0.993											
Amur, estuary, total (summer race) July–Aug., 1975	412 (10)	0.998											

[a]Only 1976.

TABLE 2. Frequencies of malate dehydrogenase phenotypes in chum populations (*N* represents number of fish studied; number in parentheses represents number of samples taken during spawning run).

Site (rivers) and time of collection of material	*N*	Phenotypes				
		A	B	C	C′	D
Naiba						
Oct.–Nov., 1969	652 (7)	0.888	0.052	0.057	—	0.003
Sept.–Nov., 1970	641 (8)	0.848	0.045	0.105	—	0.002
Oct.–Nov., 1971	281 (5)	0.875	0.032	0.089	—	0.004
Oct., 1972	88 (2)	0.795	0.148	0.057	—	—
Oct.–Nov., 1973	290 (5)	0.900	0.072	0.028	—	—
Oct., 1975	189 (4)	0.868	0.079	0.053	—	—
Oct., 1976	150 (3)	0.920	0.053	0.020	—	0.007

TABLE 2. (*Concluded*)

Site (rivers) and time of collection of material	*N*	Phenotypes A	B	C	C′	D
Oct., 1977	150	0.880	0.073	0.047	—	—
Sept.–Oct., 1978	196 (4)	0.867	0.082	0.051	—	—
Total	2493	0.875	0.061	0.062	—	0.002
Kalininka						
Oct., 1969	191 (3)	0.675	0.011	0.314	—	—
Sept.–Oct., 1970	349 (4)	0.682	0.003	0.315	—	—
Sept.–Oct., 1971	187 (4)	0.695	0.000	0.305	—	—
Sept.–Oct., 1974	392 (4)	0.610	0.000	0.390	—	—
Sept., 1975	99 (2)	0.647	0.010	0.333	0.010	—
Sept.–Oct., 1976	125 (3)	0.696	0.016	0.224	0.064	—
Sept.–Oct., 1977	150 (3)	0.693	0.000	0.307	—	—
Sept.–Oct., 1978	148 (3)	0.716	0.007	0.203	0.074	—
Total	1641	0.668	0.004	0.328	—	—
Tym′, total Oct., 1969–72, 1976	721 (1)	0.989	0.007	0.004	—	—
Buyuklinka (Poronai tributary) Oct., 1976	88 (1)	0.977	0.000	0.023	—	—
Udarnitsa, total Sept.–Oct., 1972 Oct., 1977, 1978	197 (4)	0.787	0.040	0.173	—	—
Kurilka, total Oct., 1970–72, 1977, 1978	398 (7)	0.942	0.003	0.055	—	—
Reidovaya, total Oct., 1970–72	196 (3)	0.923	0.005	0.071	—	—
Kurils, total	594	0.936	0.004	0.006	—	—
Amur, Teploe Lake (autumn race) Sept.–Oct., 1974	434 (9)	0.998	0.000	0.002	—	—
Amur, estuary, total (summer race) July–Aug., 1975	412 (10)	0.995	0.005	—	—	—

(over 350 million eggs) for acclimatization to fish hatcheries in the Naiba River basin; in some years the quantity of planted eggs exceeded the yield of the local hatcheries. Unfortunately, we have no data to characterize genetically the Naiba River population prior to making large introductions of chums from the Kalininka River. But it can be suggested that since the transferred eggs were usually collected in the Kalininka River from late September till early October, the admixture of these chums on their return to the Naiba River should be maximal in the spawning run at about the same period. In fact, a shift in the Mdh-C phenotype frequencies toward the values typical of the Kalininka population was observed in 1969–70 in the first samples from the chum stock of the Naiba River, whose spawning run begins usually later than in the Kalininka River. However, in 1971, such a shift was observed by us close to the end of the run (Fig. 5); it is interesting that in the same year the Mdh-C phenotype frequency was higher in the second half of the run in the population of the Kalininka River, also. There are also shifts in the total Alb allele frequencies (Table 1). However, these frequencies in the Naiba River population and in the other populations are very variable, and in this case it is difficult to

TABLE 3. χ^2 test for homogeneity of allele frequencies at Ldh-A^2, Alb, Ldh-B^2 loci, and Mdh phenotype frequencies in samples taken during spawning run from chum populations of the Naiba and Kalininka rivers. χ^2 for AAT and s-Idh are not presented, for they are insignificant everywhere. (*, **, *** indicate significant heterogeneity with $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.)

Populations, years	χ^2 values			
	Ldh-A^2	Ldh-B^2	Alb	Mdh-A
Naiba				
1969	3.22	22.18***	25.97***	39.4**
1970	—	64.69***	91.31***	36.5*
1971	3.52	22.87***	24.61***	17.1*
1972	0.33	1.89	1.89	0.90
1973	7.70	7.65	10.69*	—
1975	5.32	13.21**	25.2**	6.87
1976	3.22	3.28	10.68**	1.98
1977	4.46	7.28**	9.62**	6.79
1978	4.62	1.89	5.59	14.07*
Kalininka				
1969	2.20	—	—	15.00**
1970	—	52.88***	10.85*	5.37
1971	0.61	24.28***	48.25***	7.99*
1974	3.00	33.52**	8.85*	4.40
1975	0.00	0.21	—	0.00
1976	0.00	1.30	4.49	6.42
1977	0.46	6.05	0.02	6.79
1978	5.37	12.43**	22.46***	14.4**

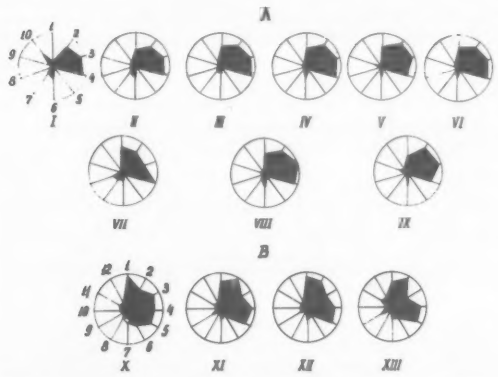

FIG. 4. Graphical representation of the genetic features of chum populations (based on phenotype frequencies at polymorphic loci). Zero in middle of circle; phenotype frequencies, on radii. A (I–IX). Ten phenotypes of four proteins studied in all populations: 1, Alb-D; 2, Ldh-B^2=F; 3, Mdh-A; 4, Ldh-A^2-A; 5, Mdh-B; 6, Alb-CD; 7, Ldh-B^2-FS; 8, Mdh-C; 9, Ldh-A^2-A'A; 10, Alb-C. I, Naiba 1969; II, Naiba 1970; III, Naiba 1971; IV, Naiba 1973 and 1975 summarized; V, Naiba 1976; VI, Naiba 1977 and 1978 summarized; VII, Kalininka, summarized data for all years; VIII, Tym', summarized data for all years; IX, Kurilka, summarized data for all years. B (X–XIII). Twelve phenotypes of six proteins were used; 1, Ldh-A^2-A; 2, Mdh-A; 3, Alb-D; 4, Ldh-B^2-F; 5, AAT-AAAA; 6, s-Idh-F; 7, s-Idh-FS; 8, Mdh-C; 9, Alb-CD; 10, Ldg-B^2-FS; 11, AAT-AAAA; 12, s-Idh-S. X, Kalininka 1976, 1977, and 1978, summarized; XI, Naiba 1976; XII, Naiba 1977 and 1978, summarized; XIII, Kurilka 1977 and 1978, summarized.

differentiate between intrapopulational heterogeneity and variations due to transplantation.

It should be noted that after 1969 the allele frequencies at the Alb locus in the Naiba shifted markedly toward values characteristic of the Kalininka River population (Table 1). However, since there are no such shifts for the other loci, it is obvious that the changes in the Alb frequencies can be only partly related to the influence of the Kalininka River chums. The changes are rather attributed to other causes, such as the sharp reduction in size of the Naiba River population and the reproduction during several years of only a part of the stock (and therefore of only a part of its gene pool). As already reported (Altukhov 1974), the coefficient of return to the Naiba for the Kalininka River chums calculated from the population-genetic data on its proportion in the Naiba River is 5 to 10 times lower than the coefficient of return to the native river.

So, while the first generation from the transferred eggs returned partly, which could be established by the corresponding phenotype and gene frequencies, the return of succeeding generations is not established by genetic data at all. It can be noted that in 1976–78 the population of the Naiba differed significantly from the population of the Kalininka River in respect to frequencies at all loci.

Consider the results of several other cases of transfer of chum eggs. In 1964 and 1967–70, about 200 million eggs from the Sokolovsky hatchery (Sakhalin, Naiba River basin) were transferred to the Teplov fish hatchery (Amur River basin). Analysis of the Teplov population was carried out in 1974, when a return of the 1970 brood (predominantly age 3+) was expected, and also a return of the second generation from the parents of 1968, a year characterized by a large proportion of chums aged 2+. In 1974, there was a larger escapement of fish to the Teplov hatchery than in previous years. The phenotype and gene frequencies at the Mdh and Ldh-A^2 loci, respectively, were recorded carefully throughout the whole spawning run (nine samples during the period from September 23 to October 10).

Table 1 shows that all loci studied proved to be practically fixed for the most frequent allele in the Teplov population, whereas in the Naiba River population these loci are polymorphic. Hence, the Teplov population does not reveal any traces of chums from the Naiba River, which means that in this case acclimatization was not a success.

Transfers of smaller quantities of chum eggs, about 3.0 and 3.5 million, respectively, were made in 1972 and 1973 from the Kuril rivers to fish hatcheries in the Naiba River basin, while 22 and 21.7 million native eggs, respectively, were used for incubation. The most characteristic distinction between these two populations was the difference in allele frequencies at the Ldh-A^2 locus. In 1976, samples from the Naiba River population displayed a clear shift of the Ldh-A^2 allele frequency towards values typical of the Kuril chums (Fig. 5). Thus, the first generation of Kuril chums produced at the hatcheries returned in sufficient amounts to the Naiba River. If we estimate the proportion of Kuril chums in the Naiba River (as was earlier done with chums of the Kalininka River, Altukhov 1974) using Ldh-A^2 allele frequencies, it turns out that in 1976 it approximated 60%. Of course, this value may be overestimated because we studied only a sample from the middle of the spawning run. It is probable that in the

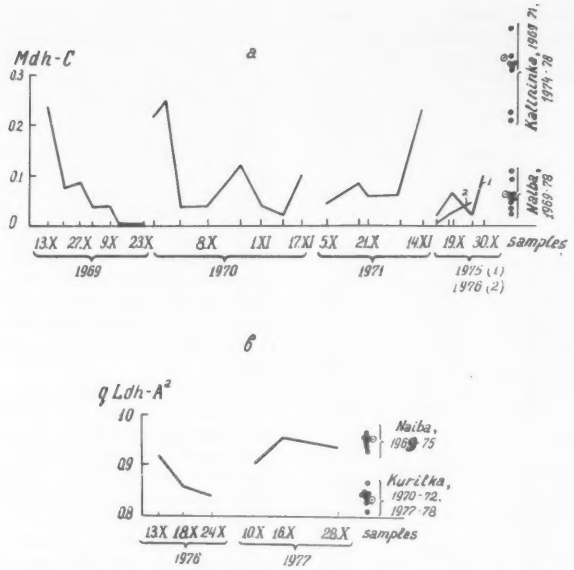

FIG. 5. (a) Dynamics of Mdh-C phenotype frequencies in samples taken throughout spawning run from the chum population of the Naiba River in 1969, 1970, 1971, 1975, 1976. (b) Dynamics of Ldh-A^2-allele frequencies in samples taken throughout spawning run from the population of the Naiba River in 1976 and 1977. On the right, values of the corresponding frequencies in the populations of the Kalininka, Naiba, and Kurilka rivers for individual years. Dot in circle, total frequency for all years of analysis.

early and late periods of the run the proportion of Kuril chums was lower. Nevertheless, if this proportion is taken as 60%, the coefficient of return for the Kuril chums (estimated from the abundance of chums in the Naiba River in 1976), will amount to about 0.17%, which is lower than that for the native Kuril stock. In fact, this coefficient was probably even lower for the reasons given above. The fact that in 1977 the Ldh-A^2 allele frequency in the Naiba River was somewhat lower, as compared to the total frequency in 1968–75, can be also regarded as evidence for the introduction of Kuril chums into the Naiba River stock. However, the fate of this acclimatization is still uncertain. At any rate, our long-term observations on chum stocks in the Kalininka and Naiba rivers clearly indicate that while in the former the stability of the population genetic structure is accompanied by a relative stability of the population size, in the latter the disturbance of the genetic structure due to the introduction of "foreign" eggs led to a significant reduction of the population size from 650000 spawners in 1968 to 57000 in 1971 (Fig. 6). In recent years, about 30 to 40 thousand fish have returned to the Naiba River for spawning.

Thus, we see that each of the chum stocks studied has its specific genetic features — characteristic frequencies of phenotypes, genotypes, and genes at certain loci. Many of these features are stable enough, at least in the generations studied. Such data permit us to regard these populations as highly independent, having achieved maximal adaptation to the particular environment in which their life history takes

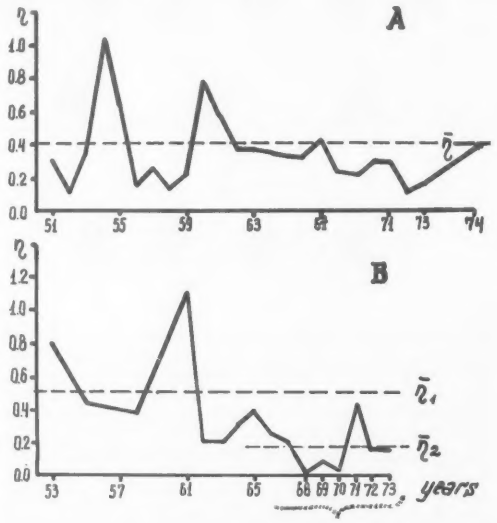

FIG. 6. Coefficients of return (%) for nonoverlapping chum generations of the Kalininka (A) and Naiba (B) rivers. The brace indicates mixed generations produced after eggs transfer.

place. The negative results of acclimatization transfers of eggs suggest a highly unique and conservative character of this adaptation (Ricker 1972; Altukhov 1974; Altukhov et al. 1981).

To study the mechanism of population adaptation to a particular environment, it is necessary to study in detail the features of the population–genetic structure of stocks.

Local Stocks as Systems of Partially Isolated, Genetically Different, Elementary Populations

We present here the most important results obtained with the redfish stock located in the Grand Bank region near Newfoundland, and with local stocks of Pacific salmon: chums and sockeye. Figure 7 shows Newfoundland and the continental slope to its right, where a population of redfish is located — a continuous belt hidden by a thick layer of seawater. The dots designate the location of trawling stations. A research vessel went along the slope, trawling continuously. From each trawl catch, fish were selected and classified by their hereditary and biological characters, such as body length, sex, age, and sexual maturity. Hereditary heterogeneity of the stock was discovered, which can be demonstrated on a so-called genogeographic map (Fig. 8). We see fields of different gene frequencies or concentrations — indirect evidence for the fact that the stock may be differentiated into smaller, genetically different substocks. Indeed, if the variation of the above-mentioned biological characters is appropriately analyzed, it is possible to find within the stock an aggregate of biologically homogeneous but still different groups (Fig. 9). These are so-called elementary populations (Fig. 10), each of them being characterized by a specific gene pool, similar to those discovered in 1963 during immunogenetic investigation of the population structure of anchovy in the Azov and Black seas (Altukhov et al. 1969a, b).

When analyzing chum salmon samples taken periodically during a spawning run, highly significant heterogeneity of phenotypic or gene frequencies is also discovered in many cases (Table 3). This hereditary heterogeneity apparently reflects the subdivision of the stock into an aggregate of genetically different subpopulations of the stock analogous to the genetic subdivision demonstrated for redfish.

Figure 11 shows the population structure of the local stock of a Pacific salmon species, the sockeye, which spawns in Lake Azabach in Kamchatka. The dots indicate the spawning sites occupied by different elementary populations. They are accessible to direct observation and therefore do not require laborious work to identify them.

What is the sense in such differentiation of a species or of parts of it, the local stocks? Are these unrelated populations, or are they parts of a whole? Observations show that subpopulations really remain parts of a whole because none of them includes all the genetic diversity that is characteristic of a whole stock, and besides they constantly interact with each other through gene exchange. Thus, a single local stock turns out to be a system of interrelated populations, the stability of such a system being a function of its inner population structure. The basic mechanisms that maintain heterogeneity and stability of a subdivided population have been established by us for the sockeye stock of Lake Azabach. The genetic structure of sockeye subpopulations belonging to the "spring" and "summer" races, and reproducing at 30 different spawning sites, was characterized during six seasons of field work with respect to the lactate dehydrogenase and phosphoglucomutase genotype and gene frequencies (Fig. 2). Some of these data have been published (Altukhov 1974; Altukhov et al. 1970, 1975a, b). Here we return to these data, together with the results of recent studies. We now have information on the genotypic structure of more than 120 subpopulations isolated from one another either in time or in space. The stability of the stock with respect to the average values of gene frequencies and their variances over several generations has been demonstrated (Table 1).

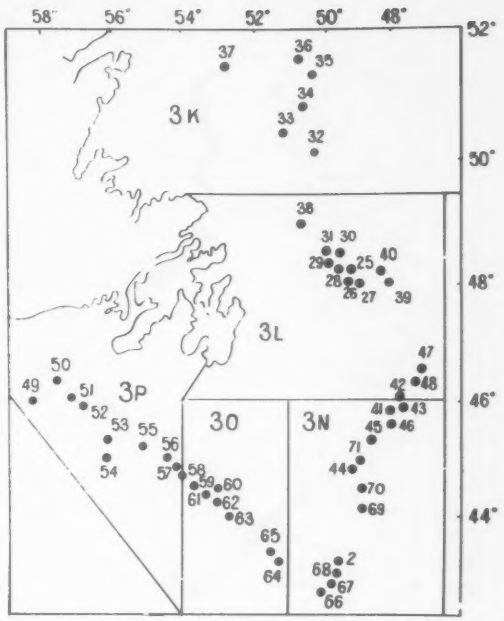

FIG. 7. Location of trawling stations on the Grand Bank and neighboring banks for deepwater redfish, *Sebastes mentella* (Altukhov 1974).

Together with the group headed by S. M. Konovalov (Institute of Marine Biology, Far-Eastern Research Center, USSR Academy of Sciences) we have studied the biological structure and the size of some sockeye subpopulations. The results show that the effective reproduction population size is 206 individuals (a harmonic mean, estimated taking into account sex ratios at individual spawning sites). On the basis of these and other ecological data, we have concluded that the actual situation observed in the case of sockeye is rather close to the island model of population structure constructed by S. Wright. Therefore it is possible to use the corresponding function for estimating population fitness in relation to the genotypes at the protein loci studied.

Wright's model postulates a stationary state in a system of populations, due to reciprocal equilibrium between the sys-

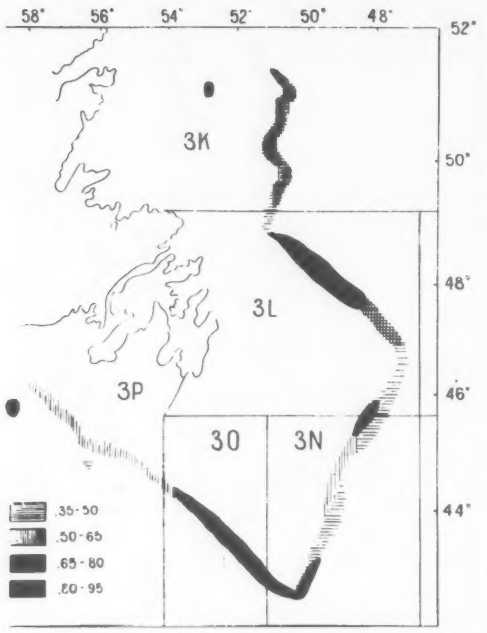

FIG. 8. Spatial heterogeneity of the deepwater redfish, *Sebastes mentella*, stock with respect to the A_2 blood group frequency in individual samples (Altukhov 1974).

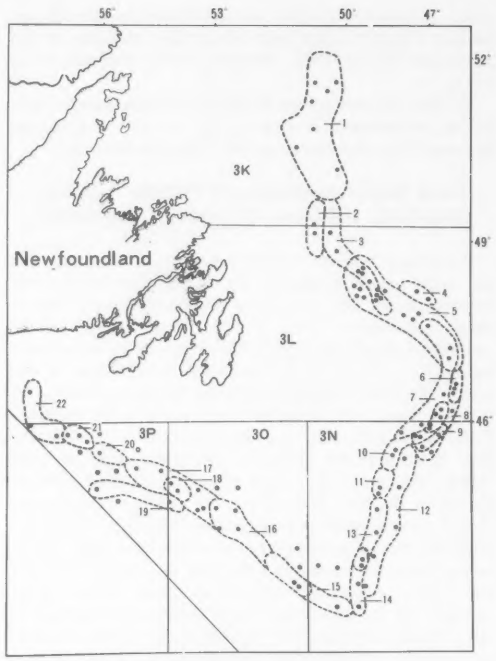

FIG. 9. Location of elementary populations of deepwater redfish, *Sebastes mentella*, on the banks off Newfoundland (1964–65). Open circles, trawling stations where samples were not taken. Contours demarcate groups of samples characterized by maximal biological homogeneity.

tematic and random pressures of evolutionary factors on its genetic structure, corresponding to the following β-distribution:

$$(1)\quad \phi(q) = \frac{C}{q(1-q)} e^{4N\int \frac{\Delta q}{q(1-q)} dq}$$

where C is a normalizing constant chosen so that

$$\int_0^1 \phi(q)dq = 1.$$

Depending on a combination of random or systematic factors determining the distribution of gene frequencies (1), it can be expressed as follows:

a) Assuming an equilibrium between isolation pressure and migration pressure:

$$(2)\quad \phi(q) = Cq^{4Nm\bar{q}-1} \cdot p^{4m\bar{p}-1}$$

where p and q are allele frequencies in subpopulations, $\bar{p}$ and $\bar{q}$ are average allele frequencies in the system, N is the genetically effective population size, and m is the migration coefficient.

b) Assuming a combined action of isolation, migration, and selection:

$$(3)\quad \phi(q) = C\bar{W}^{2N} \cdot q^{4m\bar{q}-1} \cdot p^{4\bar{p}-1}$$

where all the symbols repeat those in the previous formula, and $\bar{W}$ is the average intralocus population fitness

$$(4)\quad \bar{W} = W_{AA}p^2 + W_{AB}pq + W_{BB}q^2.$$

To build up theoretical curves of gene frequency distributions it is necessary to know the values of N, $\bar{q}$, and m. The data obtained permit the first two parameters to be estimated. The value of the migration coefficient was as used by the American authors Hartman and Raleigh (1964), who studied the intensity of migration exchange between spawning sockeye subpopulations in Brooks and Karluk lakes (Alaska) and estimated it to be not over 3%.

Calculations show that, with $m = 0.02$ for the lactate dehydrogenase locus, there is an agreement between the empirical gene frequency distribution and the expected stationary one in (1):

$$\chi^2 = 10.13 < \chi^2_{0.05} = 12.6 \qquad (df = 6);$$

at the same time, the observed distribution of phosphoglucomutase gene frequencies is significantly different from the expected stationary one:

$$\chi^2 = 35.95 > \chi^2_{0.01} = 11.34 \qquad (df = 3)$$

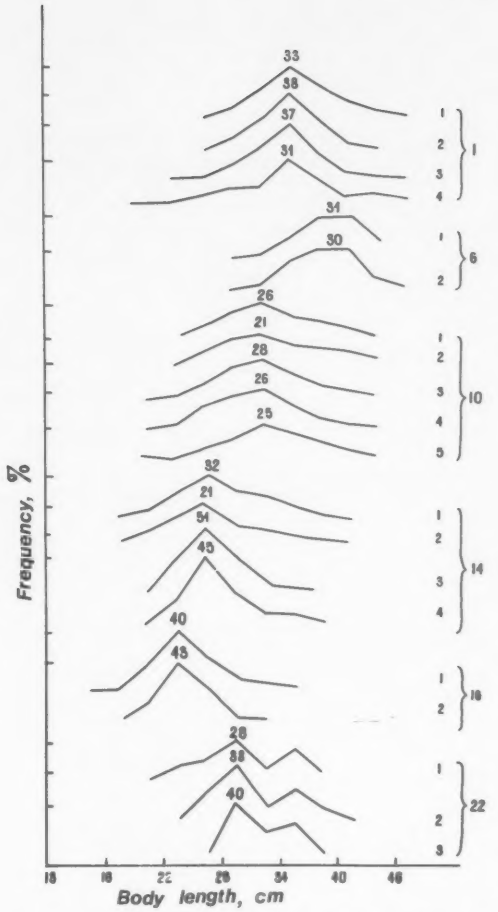

FIG. 10. Example of biological heterogeneity (for body length) of samples from accumulations of deepwater redfish, *Sebastes mentella*, belonging to elementary populations *N* 1, 6, 10, 14, 16, 22 of Fig. 9 (Altukhov 1974). Numbers over the curves are frequencies (in %) of modal class.

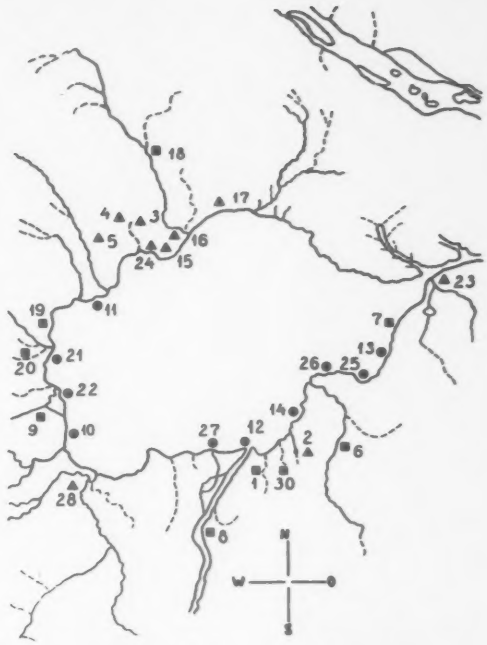

FIG. 11. Distribution of chum salmon subpopulations in Lake Azabach. (■, ▲) spawning sites of "spring race," (●) spawning sites of "summer race."

(Fig. 12). This discrepancy is accounted for by the natural selection pressure, which can be estimated by choosing the following values for the fitness coefficient in formula (3): (1) $W_{AA} = 0.987$, (2) $W_{AB} = 1.048$, (3) $W_{BB} = 0.861$. Assuming heterozygous fitness equal to 1, we have: (1) $W_{AA} = 0.942$, (2) $W_{AB} = 1.000$, (3) $W_{BB} = 0.822$.

Thus, the analysis shows that the phosphoglucomutase genotypes are under a strong pressure of stabilizing selection acting in favor of heterozygotes.

Since the exact estimation of migration coefficients for native populations of different bisexual animal species is a difficult and unsolved task, the above values of fitness required checking by a suitable and independent method. Two methods can be used. First, differences in the interpopulational variances of gene frequencies of the two loci can be used to suggest their more or less neutral character and, thus, to estimate the *Nm* parameter in formulae (2) and (3), through the variance of frequencies at the locus characterized by the widest frequency range (Ldh-B^1). Second, since the stock as a whole is characterized by stability of gene frequencies at both loci through generations, it is possible to estimate the fitness of genotypes directly from the ratio of their observed frequencies to those theoretically expected from the Hardy–Weinberg formula. We used both methods, and both showed practically a complete coincidence of *W* values with those obtained by independent methods.

In addition, agreement between the empirical and theoretically expected distributions of frequencies at the lactate dehydrogenase locus became more satisfactory ($\chi^2 = 3.04 < \chi^2_{0.05} = 5.35$; df = 6) when we introduced into the stability formula *W* values that reflect the pressure of stabilizing selection: $W_{BB} = 0.98$, $W_{BB'} = 1.00$, and $W_{B'B'} = 0.97$. However, more detailed studies of distributions of lactate dehydrogenase genotypes in different years and at spawning grounds of different types have revealed a more complicated pattern of selection for this locus. At the present stage of analysis it can be concluded that the sockeye subpopulations of the spring race, which reproduce in streams, are subjected to a stronger selection pressure than the subpopulations of the summer race, which are adapted mainly

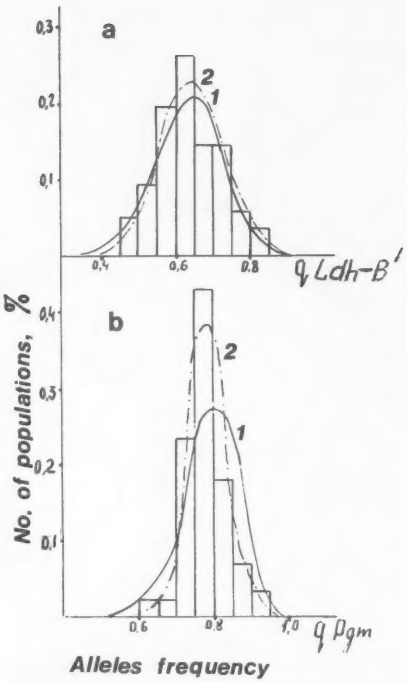

FIG. 12. Distribution of lactate dehydrogenase (a) and phosphoglucomutase (b) gene frequencies in elementary sockeye salmon populations in Lake Azabach. Histograms, empirical distributions; curves, theoretical distributions.

$$(1)\quad \phi(q) = Cq^{4Nm\bar{q}-1}(1-q)^{4Nm\bar{p}-1}$$

$$(2)\quad \phi(q) = C\bar{W}^{2N}q^{4Nm\bar{q}-1}(1-q)^{4Nm\bar{p}-1}$$

Abscissa, gene frequency. Ordinate, number of populations (% of the total number studied) falling in the corresponding frequency range.

to reproduction in lakes (Rjabova et al. 1978). A correlation of the frequency of one of the lactate dehydrogenase alleles with water temperature during spawning has also been observed (Titova 1979).

Moreover, analysis of genotype distributions for the two loci simultaneously reveals clear genetic differences between male and female sockeye: the fitness of females, apparently related to a particular heterozygosity optimum, remains more or less constant through the years, while male heterozygosity varies in time and between age- and size-groups. Males are also characterized by a higher frequency of rare genotypic combinations. On the whole, a clear relationship is observed between the distribution of spawning fish by body size and their genetic features.

Thus, the above population–genetic parameters of several sockeye generations (Table 4) and the allele distributions (Fig. 12) show that the local sockeye stock of Lake Azabach is, as was expected, a genetically stable system, despite the wide spatial isolation of its populations.

It is obvious that efficient fishery management and preservation of genetic stability of population systems is possible only if their hereditary heterogeneity is taken into consideration. In the next section this question will be considered in detail.

Strategy of Fishery Management Providing for Maintenance of a Population System as a Whole

Studying in detail a local stock of sockeye, we saw that its genetic stability is the result of a reciprocal balance between isolation, migration, and selection. Each of these factors can lead to significant reorganization of the gene pools of the elementary population units. However, at the level of the subdivided population as a whole, a combined action of the same forces is converted into genetic stability of the population system. It is clear that in practice it matters very much what population we deal with: either with an elementary group, the behavior of which is extremely difficult to forecast because of purely random factors, or with an aggregate of such populations, which is characterized by stability from year to year and therefore is accessible to long-term forecasting with respect to its important biological features. Disregarding external influences of a severity comparable to natural catastrophies, for the purpose of maintaining long-term stability it is obviously necessary to use a comprehensive approach to a population system, considering all its components.

Let us consider how the observance of, or failure to observe, this principle in the practical work of a hatchery influences population biology, taking the chum stock of the Kalininka River as an example. An indicator of subpopulation structure of the stock will be the sex ratio in samples, a specific population parameter that differs from the equilibrium ratio in elementary fish populations (Lebedev 1967; Altukhov et al. 1969b, Altukhov 1974).

In this case we shall use values of male frequencies in samples taken during a spawning run, summarized by 10-d periods. If the structure of this population is not yet destroyed, we have grounds to expect variation in the sex ratio as management efforts are transferred from the head to the tail end of the run. In spite of the fact that values of the averaged 10-d periods should distort the expected dynamics of the character (individual subpopulations cannot help mixing, at least partly, in the fence zone), our supposition proves to be true (Fig. 13). The material presented, using only the age-group that predominates in the spawning part of the stock, reveals sharp changes in the frequency of males during the spawning run. In agreement with the known features of chum biology, an excess of males is observed at the start of the spawning migration; in the middle of the spawning run the sex ratio achieves equality; and at the end females prevail. Since thousands on tens of thousands of spawners may be counted in a 10-d period, the confidence intervals of male frequency values are very narrow. They are larger at the beginning and at the end of management actions, because samples are small when the fish are just beginning the spawning run, and also when it draws to a close. The intervals are shown as vertical bars in Fig. 13a. In Figure 13, b–d, the intervals were similar, and the seasonal trends in the frequency of males were no less significant.

TABLE 4. Basic population–genetic parameters of a series of generations of the sockeye stock of Lake Azabach.[a]

Locus	Year	K	N	$\bar{q}$	σ_q^2	χ^2 test for homogeneity of dispersions (Bartlett's criterion)	χ^2 test for homogeneity of the stock (df)
Ldh	1971	14	737	0.6545	0.0074		$50.18 > \chi^2_{0.01}\ (13) = 27.69$
	1972	20	1022	0.6114	0.0048		$37.53 > \chi^2_{0.01}\ (19) = 36.19$
	1973	21	1007	0.6478	0.0078		$65.11 > \chi^2_{0.001}\ (20) = 45.3$
	1974	14	676	0.6612	0.0076	$1.09 < 1.15_{0.95}(5)$	$45.59 > \chi^2_{0.001}\ (13) = 34.5$
	1977	19	934	0.6552	0.0084		$69.34 > \chi^2_{0.001}\ (18) = 42.3$
	1978	23	1244	0.6455	0.0071		$76.62 > \chi^2_{0.001}\ (22) = 48.3$
Pgm	1971	14	748	0.7929	0.0028		$22.57 > \chi^2_{0.05}\ (13) = 22.38$
	1972	20	1004	0.7675	0.0019		$21.76 > \chi^2_{0.25}\ (19) = 22.72$
	1973	21	981	0.7899	0.0041		$41.36 > \chi^2_{0.01}\ (20) = 37.57$
	1974	12	546	0.7838	0.0037	$7.35 < 9.24_{0.1}(5)$	$23.02 > \chi^2_{0.05}\ (11) = 19.7$
	1977	19	936	0.8119	0.0032		$39.21 > \chi^2_{0.01}\ (18) = 34.8$
	1978	23	1241	0.7732	0.0025		$35.78 > \chi^2_{0.05}\ (22) = 33.9$

[a] K, number of populations studied; N, number of fish analyzed; $\bar{q}$, average gene frequency; σ_q^2, interpopulation variance of gene frequencies.

As the figures demonstrate, the chum stock of the Kalininka River can be divided, for pragmatic purposes at least, into three components: (1) with an excess of males, (2) with an even sex ratio, and (3) with an excess of females.

Let us try to estimate the contribution of each of these components into the total egg yield of the hatchery. To this end, we shall consider the data for those generations that, as a whole, have an even sex ratio, but at the same time are characterized by a rather high variation of this character in time. This will make it possible to determine the volumes of egg yields in the first half of the spawning run (September) and in the second half (October). The following data are obtained:

Time of spawning run	Generations: 1957 males, %	1957 egg yield (million)	1959 males, %	1959 egg yield (million)	1965 males, %	1965 egg yield (million)	1966 males, %	1966 egg yield (million)
September	62	4.9	58	24.3	59	60.5	57	57.1
October	51	35.5	49	48.9	52	112.1	52	76.4

Of course, these data reflect the natural situation only roughly. Nevertheless, a general tendency is clear: more intensive collection of eggs[2] occurs in the second half of the run in accordance with the number of female spawners. In the opinion of fish breeders at the Kalininsky hatchery, approximately half of the stock really falls in the middle part of the run, and the other half is distributed between the beginning and the end of migration.

Thus, when collecting reproductive products for hatchery purposes, simultaneously controlling the sex ratio in samples, 25% of eggs should be collected at the beginning of the migration of spawners into the river, 50% from the middle part of the run, and 25% at the end. This scheme should be effective even if each of the three roughly distinguished parts of a stock has, as seems to be true, its own inner subpopulation structure. The above statement is supported by our data for anchovy, whose five elementary populations, out of 11 distinguished, have approximately equal sex ratios (Altukhov et al. 1969b), and also by analogous results obtained on the sockeye of Lake Azabach and on the Newfoundland redfish stock (Altukhov 1974).

Disregard of the population organization of a local stock in practical management can lead to important changes of its biological features. This can be proved by the graphs showing the variation of male frequency in the Kalininka River population (Fig. 13). In all graphs, the thickened parts of the abscissa indicate the time of egg collection. It is evident that during the early period of the hatchery's operation, eggs were as a rule collected from all the migrating fish, but later, as the size of the stock grew, it was enough for the hatchery to collect eggs mainly from the subpopulations that came in first from the sea and were characterized, as has been mentioned, by an excess of males, and from only part of the populations with an even sex ratio. This was the situation in 1957, 1958, 1964, 1965–67, 1968, 1970, and 1971. A reliable correlation between the frequency of males (or females) in that part of the stock from which eggs were collected in the given year, and their frequency in the whole run 4 years later can serve as a good illustration of the statement made at the beginning of this paper about the biological features of populations being a function of their gene pools, i.e. inheritable. And in fact, this correlation coefficient, estimated assuming a linear pattern of correlation, turns out to be +0.56 (N = 17), which is significant at the P = 0.01 level (Fig. 14).

The correlation discovered is only moderate, but it should be remembered that it was obtained with a deliberately simplified age structure of the stock[3] and without taking into consideration a compensatory mechanism that is theoretically possible, but not accessible to investigation, namely the birth of individuals of a sex opposite to the one in excess (Hamilton 1967).

In accordance with the correlation, the chum stock of the Kalininka River, which at the beginning of the hatchery's operation had an even sex ratio or a deficiency of males in

[2] The values presented reflect total egg yields of the Kalininsky hatchery and of hatcheries located on other rivers.

[3] Four-year individuals prevail in the spawning chum stock; however, 3- and 5-yr individuals are also present.

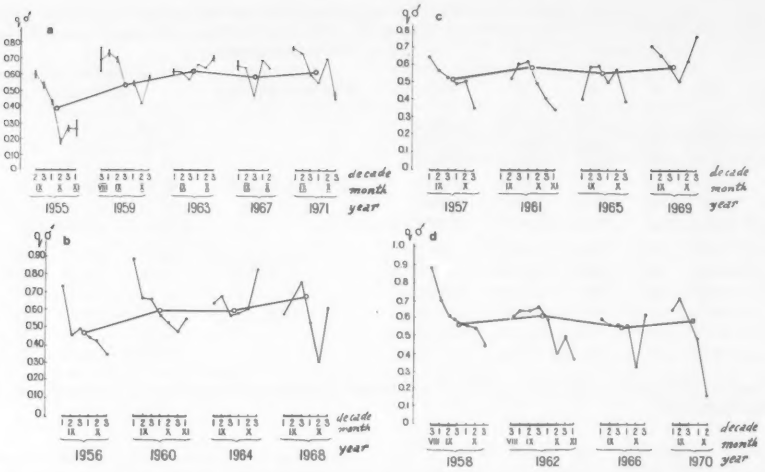

FIG. 13. Time dynamics of sex ratios in four successive generations (a–d) of chum stock of the Kalininka River. Thickening of the abscissa indicates time of egg collection in individual years. Solid circles, male frequency per 10-day period; open circles, male frequency in the stock as a whole.

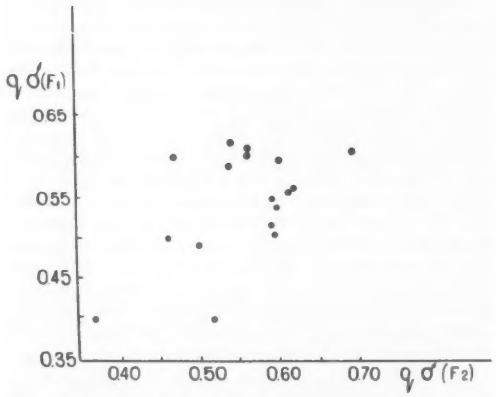

FIG. 14. Correlation between the proportions of males among chum spawners used for hatchery purposes in the given year (ordinate) and in the whole stock of the Kalininka River 4 yr later (abscissa), $r = 0.5625$; $P < 0.01$.

some generations, now has an excess of males that reaches 10 to 20% in some generations.

Nevertheless, in spite of the unfavorable tendency discovered, the Kalininka River stock is characterized by genetic stability which is achieved through a proper distribution of management efforts, at least in some generations, over all the components of their population structure.

In direct contrast is the stock of the Naiba River, the genetic stability of which has been disturbed because its population organization has been disregarded, and this, as a consequence, has affected its production potential. This stock also displays deformation of the sex structure due to increase in the proportion of females, as was observed, for example, in the 1968 run (Altukhov 1974).

On the basis of the above facts, which are apparently of great biological significance, a simple principle of fishery management in natural water basins can be recommended: to distribute management efforts over all elementary population units composing the structure of stocks. It is clear that, since population gene pools appear to be distributed among at least partially isolated subpopulations, this principle would be more efficient for regulating fishing and in attempting acclimatization than the existing approaches that disregard specific features of the population–genetic structure of a species.

Despite criticism of our concept (Malinovsky and Mina 1976; Mina 1978; Altukhov 1977), its importance as a principle for the fishing industry is admitted by many specialists (Konovalov 1972; Konovalov et al. 1975; Starobogatov 1975; Dubinin 1976; Aronshtam et al. 1977; Kirpichnikov 1979; Mashurov 1979), and the approach itself has been registered as invention (Altukhov et al. 1972).

Conclusion

Historically, population genetics has had as its main interest evolutionary problems in biology, primary attention being placed on different aspects of genetic dynamics of populations in space and time. This has led to the creation of a carefully elaborated probability theory of evolutionary process expressed in genetic terms; but for a long time it distracted the attention of researchers from the fact that natural populations are, in addition, the basic units for practical management, the success of which is associated not so much with the question of their evolution as with the factors and conditions of stability.

Indeed, comparative studies of the historically established hierarchic structure of a species show that, in spite of the genetic reorganizations that occur in elementary populations, the totality of such populations remains stable in time and in

space. Thus, from the point of view of genetic stability there are different types of populations. In several fish species having very different ecologies, it is possible to distinguish at least two levels of population hierarchy that are qualitatively different in their genetic features. On the one hand there are genetically stable population systems corresponding to the model of subdivided populations; and on the other, more elementary and sometimes highly variable population units which are the structural components of such systems, and corresponding most closely to the model of a "Medelian population," which is traditionally considered as the elementary unit of evolutionary process. To the extent that it can be assumed that these two kinds of populations play no independent role in nature, the tempo of microevolution should be correlated with the possibilities for transformation of the genetic structure of a population system which remains stable under the widest range of environmental changes (Altukhov and Rychkov 1970; Altukhov and Pobedonostseva 1978, 1979a, b; Altukhov and Bernashevskaya 1978; Altukhov et al. 1979).

The mechanisms of genetic stabilization of natural populations in the course of their repeated self-reproduction in successive generations and over their entire range seem to be universal enough, in the sense that such stability is everywhere determined by an equilibrium established between the same factors — selection, random genetic drift, and gene migration. Differences can exist only in the relative roles of these three, depending on the genotypes studied and on the historically established features of population structure.

As for practical consequences resulting from the fact of the systemic organization of natural populations, at least three main possibilities are apparent.

The first is the possibility of constructing a natural classification of species subdivisions and unifying the terminology.

Apparently, no matter how simple or complex intraspecific differentiation may be, it is always possible to distinguish at least two basic structural levels, namely the population system and its structural components. From this point of view, such interchangeable terms as "population," "stock" (Russian *stado*), and "isolate" are used to denote the system, and terms "subpopulation," "elementary populations," "subisolate," and others, for its structural components.

Second, evidence for the relative independence of stocks and genetic differences between them open new possibilities for their rapid identification during different periods of the annual cycle. To organize a regulated fishery, we should have clear knowledge of the population structure of the species concerned; we should know the degree of isolation of populations and the tempo of their reproduction (average generation length); and finally, on the basis of that structure, provide the fishing industry with well-founded recommendations so that the intensity of fishing should not exceed the tempo of natural (or artificial) reproduction.

Third, the discovery of the genetic subdivision of local stocks of fish species with different ecologies is of prime importance not only for fisheries but also for artificial reproduction of the stocks — either in hatcheries, in aquaculture, or in case of restoring populations destroyed by extreme anthropogenic pressure.

Based on clear knowledge of the features of the inner structure of such a system, by distributing fishing and management efforts evenly and proportionally over all its components, we will achieve efficient management that provides for long-term maintenance of a natural population. But if elementary populations are treated as a whole, their dependent position in the structure of a species being disregarded, the result can only be the disintegration of the population system.

It is clear that the more complex is the organization of a subdivided population, the longer it can withstand external influences, and from this point of view, the species as a whole should be regarded as the basic unit for management. However, under conditions of limited practical activity, the necessary effects can be also achieved at lower levels of the population hierarchy, provided their groupings are not accidental, but are determined by a necessary complex of life history data.

Therefore, population genetics opens wide possibilities for uniting the efforts of biologists working in different areas for the purpose of developing a universal strategy of balanced management of fish resources. Preservation of genetic stability of intact population systems, restoration of those with structure that has been disturbed, and finally, creation of new systems, under proper conditions, are the main tasks to which our efforts must be directed.

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Origin and Geography of the Fish Fauna of the Laurentian Great Lakes Basin[1]

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The native fishes of the Great Lakes basin consist of 153 species, 64 genera, and 25 families. The total ichthyofaunal lists for the several lakes and (in parentheses) their tributary basins are as follows: Nipigon (and tributaries), 40; Superior, 53 (82); Michigan, 91 (135); Huron, 90 (112); St. Clair and Detroit River 108; Erie, 106 (125); Ontario, 95 (125). (These totals include 21 introduced species, most named species of ciscoes and chubs, and the blue pike (*Stizostedion vitreum glaucum*).)

Several areas show notable within-species differentiation. Tributaries to Lake Ontario are part of a zone of secondary contact of a few small, nonmanaged, subspecies that entered the basin from both eastern and western glacial refugia. In the Great Lakes themselves, stocks of lake trout (*Salvelinus namaycush*), ciscoes, walleyes (*Stizostedion vitreum vitreum*), and a few nonmanaged species stem from differentiation within the basin or reflect interglacial events that occurred in Mississippi refugia.

Species distribution patterns suggest colonization of the Great Lakes by 122 kinds solely from Mississippi basin refugia, 14 kinds only from Atlantic drainage refugia,and dual refugia for at least 18 kinds. Geological evidence provides some support for this interpretation. It is unlikely that any species colonized the Great Lakes from an Alaskan refuge in the past 14 000 yr.

The ciscoes and chubs of the genus *Coregonus* include numerous genetically differentiated stocks, some of which may predate the opening of the Great Lakes in the past 14 000 yr. This conclusion is based on the occurrence in Lake Nipigon and Lake Superior of several forms that must have colonized prior to 9000 yr ago when the last access existed from Lake Superior to Lake Nipigon. At least four and perhaps up to eight forms of Great Lakes coregonines probably survived (or differentiated during) the last glaciation south of the ice in proglacial waters at the heads of major river systems. There is no evidence to support the hypothesized post-Wisconsinan dispersal of any of these forms from a northwestern refugium or their Pleistocene derivation by introgression with a Eurasian species.

Despite the evidence for some long-standing genetic differentiation within *Coregonus*, morphological and biochemical characters fail to support the unequivocal recognition within the Great Lakes of more than one to four current biological species (apart from *clupeaformis*). The presently recognized species are groups of stocks whose position in the classification system is problematical. The named groups (two of which are extinct) included numerous stocks that were (or are) isolated by homing behavior specific to time and place. The lack of intrinsic reproductive isolation among forms increases their vulnerability to extinction because rare forms apparently hybridize with common forms spawning at adjacent times or places.

Key words: biogeography, *Coregonus*, fish, Great Lakes, introduced fishes, Pleistocene, species, subspecies

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On compte dans le bassin des Grands Lacs 153 espèces de poissons indigènes, appartenant à 64 genres et 25 familles. La faune ichtyologique totale des nombreux lacs et (entre parenthèses) les bassins de leurs affluents sont les suivants : Nipigon (et tributaires) 40, Supérieur 53 (82), Michigan 91 (135), Huron 90 (112), St. Clair et rivière Détroit 108, Érié 106 (125), Ontario 95 (125). (Ces totaux incluent 21 espèces introduites, la plupart des

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espèces nommées de ciscos et de « chubs », ainsi que le doré bleu.)

On observe dans plusieurs régions des différences intraspécifiques notables. Les tributaires du lac Ontario font partie d'une zone de contact secondaire pour quelques petites sous-espèces non gérées qui pénétrèrent dans le bassin en provenance de refuges glaciaires tant de l'est que de l'ouest. Dans les Grands Lacs eux-mêmes, on trouve des stocks de touladis, de ciscos, de dorés jaunes et de quelques espèces non gérées qui doivent leur origine à une différenciation à l'intérieur du bassin ou qui reflètent des événements interglaciaires qui sont survenus dans des refuges mississippiens.

La distribution des espèces suggère que les Grands Lacs ont été colonisées par 122 sortes de poissons provenant exclusivement de refuges du bassin du Mississippi, 14 sortes seulement de refuges du bassin de l'Atlantique et au moins 18 sortes de refuges doubles. Les données géologiques semblent appuyer cette interprétation. Il est peu probable qu'une espèce ait colonisé les Grands Lacs à partir d'un refuge de l'Alaska dans les 14 000 dernières années.

Parmi les ciscos et les chubs du genre *Coregonus*, on compte de nombreux stocks génétiquement distincts, dont certains peuvent même prédater l'ouverture des Grands Lacs dans les 14 000 dernières années. Cette conclusion repose sur la présence, dans les lacs Nipigon et Supérieur. De plusieurs formes qui doivent s'y être établies il y a plus de 9 000 ans, alors qu'existait la dernière voie d'accès au lac Nipigon depuis le lac Supérieur. Il est probable qu'au moins quatre et même jusqu'à huit formes de corégoninés des Grands Lacs aient survécu ou se soient différenciés pendant la dernière glaciation au sud de la glace, dans des eaux proglaciaires, à la tête des principaux réseaux fluviaux. L'hypothèse d'une dissémination subséquente à la glaciation du Wisconsin d'une de ces formes à partir d'un refuge du nord-ouest ou de leur dérivation au cours du Pléistocène par introgression avec une espèce eurasienne n'est appuyée d'aucune preuve.

En dépit de signes d'une différenciation génétique ancienne au sein du genre *Coregonus*, les caractères morphologiques et biochimiques ne permettent pas de reconnaître, de façon non équivoque, dans les Grands Lacs plus de une à quatre espèces biologiques actuelles (autres que *clupeaformis*). Les espèces présentement reconnues sont des groupes de stocks dont la position dans le système de classification est problématique. Les groupes nommés (dont deux sont éteints) comprenaient de nombreux stocks qui étaient (ou qui sont) isolés par un homing spécifique quant à l'époque et à l'endroit. L'absence d'isolation reproductrice intrinsèque parmi les formes les rend plus vulnérables à l'extinction parce que, semble-t-il, les formes rares se croisent avec les formes communes frayant à des époques et à des endroits adjacents.

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THE Laurentian Great Lakes constitute the greatest freshwater reservoir on our planet. Each of the five principal lakes of the system is ranked among the nine largest freshwater lakes in the world and there are in addition thousands of smaller lakes and extensive stream development in the basin (Fig. 1). Consideration of the biota of the area is governed by its geological youth; the entire basin was blanketed in the Wisconsin Glaciation. Exposure from the mantle of ice dates only from perhaps 14 000 yr at the southern edge to some 9000 yr in the northern part of the basin.

Thus, the ichthyofauna is of recent origin in the area. The major component arrived by active immigration, utilizing open-water channels that connected peripheral, ice-free refugia and proglacial waters with the newly created aquatic habitat. Most of the wave of immigrants probably came early, when major waterways were readily available, but some recent intrusions likely occurred through stream capture and headwater crossovers in swamps or marshes astride watersheds (e.g. Maumee–Wabash, Fox–Wisconsin, Mohawk–Hudson). Potentially, although with a time constraint, the vast new habitat provided an environment for the evolutionary emergence, in situ, of new stocks differentiated from the parental invaders. Finally, a third mode of access was provided by the direct intervention of man and his activities. The Great Lakes were new and ecologically unsaturated, and introduced fishes have been exceptionally successful, many having encountered favorable habitats they otherwise would have been denied.

Despite recent occupation by fishes and the northern location of the Great Lakes, lying chiefly between the 40th and 50th parallels of latitude, the fish fauna is relatively large and diversified. It numbers 174 species, classified in 71 genera and 28 families (Table 1). This large assortment results in large part from the multiple avenues for northward postglacial dispersal through major waterways flowing southward into the Mississippi River basin, center of one of the great temperate freshwater fish faunas of the world.

Late Pleistocene Geological History of the Great Lakes

The following account covers the postglacial history of the past 14 000 yr. It is compiled primarily from Prest (1970), Zoltai (1965, 1967a, b), Farrand (1969), and Flint (1971). We do not review the geological data, but are concerned with inferred lakes and their connections as fish habitats and dis-

91°
87°
83°
79°
75°
49°
47°
45°
43°
41°
25 0 25 50 100 200
SCALE OF MILES
50 0 50 100 200 300
SCALE OF KILOMETRES
LAKE SUPERIOR
LAKE MICHIGAN
LAKE HURON
LAKE ONTARIO
LAKE ERIE

FIG. 1.

TABLE 1. Composition of the Great Lakes fish fauna.

Families	Genera	Species	Subspecies	Alien Forms
Petromyzontidae	3	5	5	0
Polyodontidae	1	1	1	0
Acipenseridae	1	1	1	0
Lepisosteidae	1	3	3	1
Amiidae	1	1	1	0
Anguillidae	1	1	1	0
Hiodontidae	1	1	1	0
Clupeidae	2	2	2	1
Salmonidae	6	20[2]	20[2]	6
Salmoninae	(3)	(9)	(9)	(6)
Thymallinae	(1)	(1)	(1)	(0)
Coregoninae	(2)	(10)[2]	(10)[2]	(0)
Osmeridae[1]	1	1	1	1
Umbridae	1	1	1	0
Esocidae	1	4	4	0
Cyprinidae	17	53	55	4
Catostomidae	8	16	17	0
Cobitidae[1]	1	1	1	1
Ictaluridae	3	11	11	1
Aphredoderidae	1	1	1	0
Percopsidae	1	1	1	0
Gadidae	1	1	1	0
Cyprinodontidae	1	3	4	0
Poeciliidae[1]	1	1	1	1
Atherinidae	1	1	1	0
Gasterosteidae	3	3	3	0
Percichthyidae	1	3	3	2
Centrarchidae	4	12	12	3
Percidae	5	21	23	0
Sciaenidae	1	1	1	0
Cottidae	2	4	4	0
Totals 28	71	174[2]	180[2]	21
Native 25	64	153[2]	159[2]	

[1]Family introduced.
[2]If the various ciscoes are all regarded as stocks of *Coregonus artedii* (see p. 1555–1558), these figures should be reduced by six.

persal routes. Pleistocene history of these basins prior to 14 000 yr ago is unknown except that each of the glaciations created a biogeographically anomalous situation. All species now in the area colonized within the past 14 000 yr. Furthermore, conditions like the current interglacial, with many of the present kinds of animals, must have existed in the region several times in the last 2 million years, only to be erased by each advance of the ice.

In general, extensive volumes of water harboring fish existed around the periphery of the glaciers at the heads of rivers. As advancing glaciers overrode existing lakes, and as retreating glaciers gave way to new lakes, populations of fishes continued to exist in slowly shifting habitats. Local extinctions and recolonization by dispersal were no doubt common in these refugia.

We summarize the history of the lakes in four stages: (1) the periglacial and Algonquin stage, 14 000–10 600 yr ago, with diverse outlets initially to the south; (2) the stage of maximum isolation of numerous lakes, 10 600–8100 yr ago, with major drainage to the St. Lawrence; (3) the broadly connected (approximately Nipissing) stage, 8100–6000 yr ago, ending with the Nipissing three-outlet phase; and (4) the modern configuration of the lakes, 6000 yr ago to the present (Fig. 1).

THE PERIGLACIAL AND ALGONQUIN STAGE, 14 000–10 600 YEARS AGO

Periglacial lakes began in the Michigan basin (L. Chicago) and Erie and Huron basins (L. Maumee), 14 000 yr ago (Fig. 2). Drainage was south through the Chicago outlet and the Illinois–Mississippi rivers and the Maumee–Wabash–Ohio–Mississippi rivers, respectively. As the ice retreated northward and waters expanded into more of the Huron basin 13 600 yr ago (L. Arkona), crustal rebound closed the Maumee outlet and the Grand River began to carry waters from the Huron to the Michigan basin (Fig. 3). Lakes in the Erie and Huron basins were confluent until 12 700 yr ago. At this time, Lake Agassiz had appeared, a temporary lake (Keweenaw) occupied part of the Superior basin, and precursors of Lakes Huron and Michigan were united as Lake Algonquin. All three systems drained to the Mississippi, but fluvial connections existed to Lake Erie and to the Ontario basin (Lake Iroquois) as well (Fig. 4). Lake Iroquois drained to the Hudson River. A small lake in the Ontario basin (Lake Newberry) connected to the Susquehanna basin 13 600–13 200 yr ago (Fig. 3). (However, fish distributional evidence requires a connection between the Great Lakes and the Susquehanna drainage, discussed below.)

The Belleville–Fort Ann phase was a large expansion from the Ontario basin northeast into the St. Lawrence Valley 12 000 yr ago. It received discharge from Lake Algonquin (Michigan and Huron basins) through the Kirkfield outlet system (Trent Valley) (Fig. 4).

Lake Agassiz and Lake Keweenaw (Superior basin) were connected by southeast-flowing rivers 12 200 yr ago (Elson 1967; Zoltai 1967a, b; Prest 1970). However, Valders ice filled the Superior basin and covered most of the Michigan basin 11 800 yr ago (Fig. 5). By 10 900 yr ago ice had again retreated and Lake Duluth occupied the Superior basin, making it an important biogeographic entity for the first time (Fig. 6). Connections existed between Lakes Agassiz and Duluth, and lacustrine connections developed between Duluth and the Michigan basin through the Au Train–Whitefish Straits north of Green Bay 11 200 yr ago. Lake Duluth drained to the Mississippi River. The earliest stages of the lake were higher (elevation of up to 1085 ft (331 m)) than at any subsequent time (Farrand 1969) and it was at this time that fishes were able to colonize Lake Superior tributaries above their falls.

The last phase of this early stage of lake history was the opening, by deglaciation, of the North Bay outlet from northeast Lake Algonquin to the Champlain Sea 11 200 yr ago (outlet location shown in Fig. 7), beginning the period of rapid decline in lake levels.

FIG. 1. The Great Lakes drainage basin. Lakes Nipigon (north of Lake Superior) and St. Clair (between Huron and Erie) not labeled. Gaps in the line marking the boundary are points of known or inferred drainage connections.

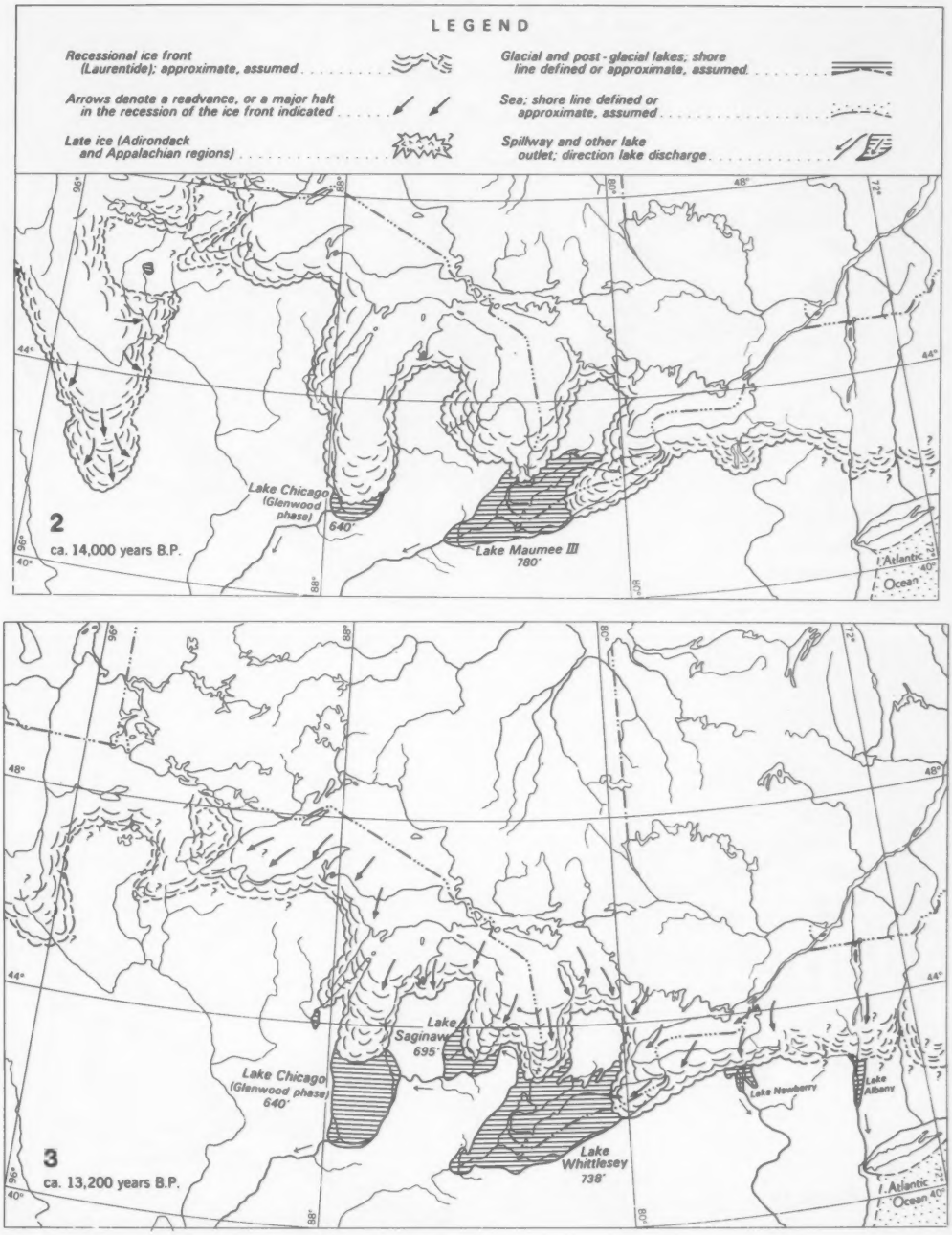


FIG. 2, 3. Earliest stages of the Great Lakes 14 000 to 13 200 yr ago, showing drainage to the Mississippi, Susquehanna, and Hudson. (Reprinted with permission, from Prest 1970.)

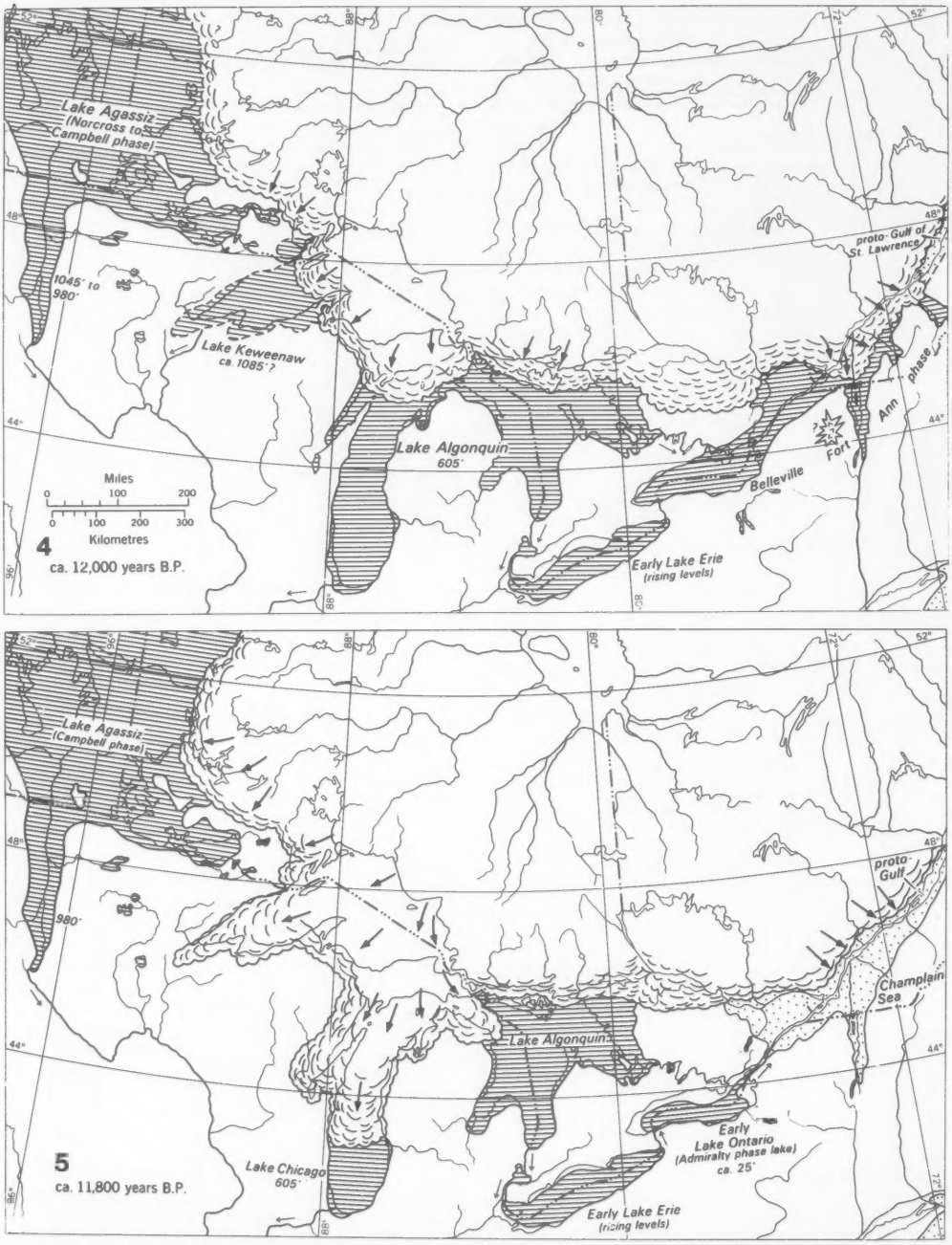


FIG. 4, 5. Development of Lake Agassiz with drainage to the Mississippi system. Direct connection existed between Lake Algonquin and the Ontario basin. Lake Kewennaw was eliminated by the Valders advance 11 800 yr ago. (From Prest 1970.)

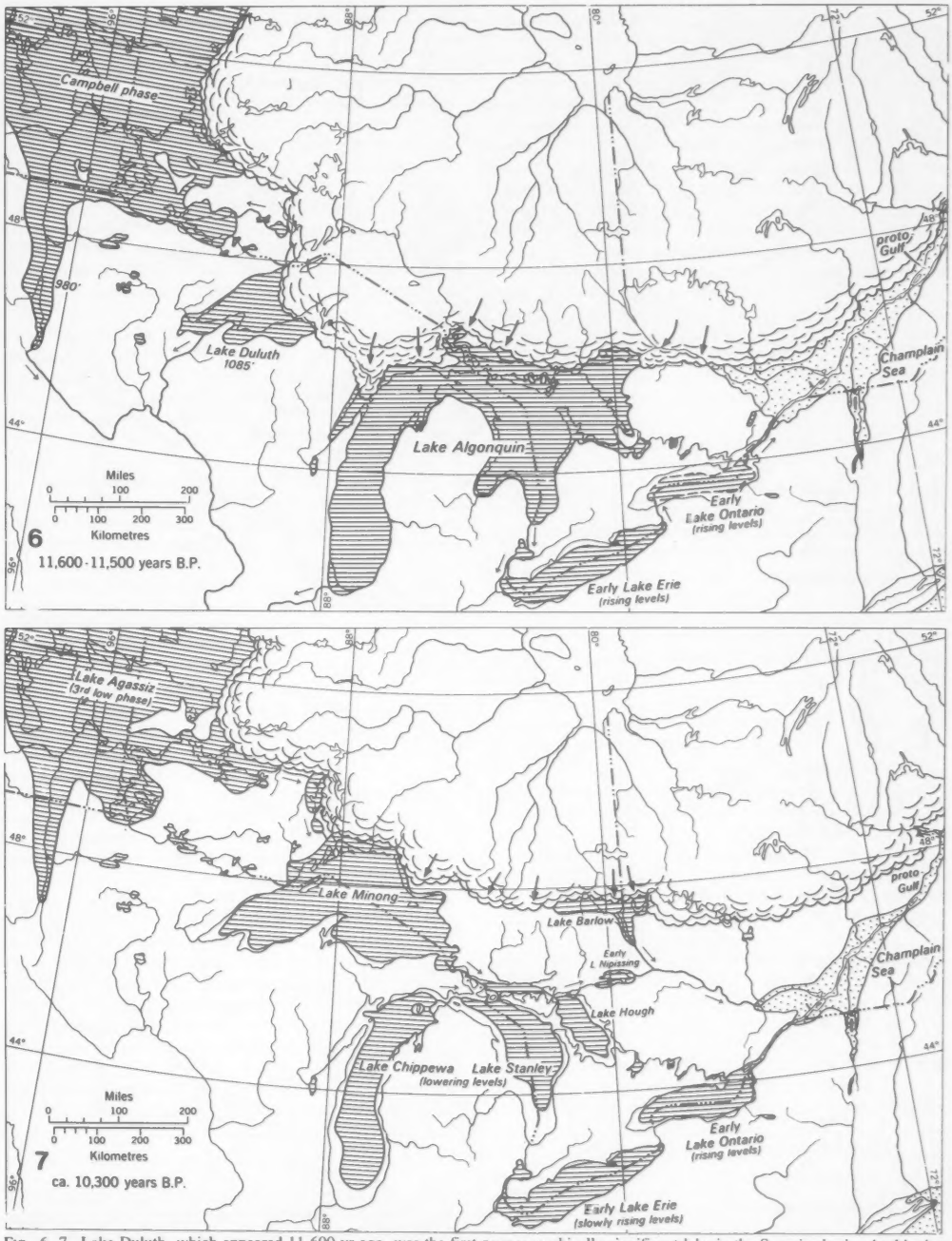
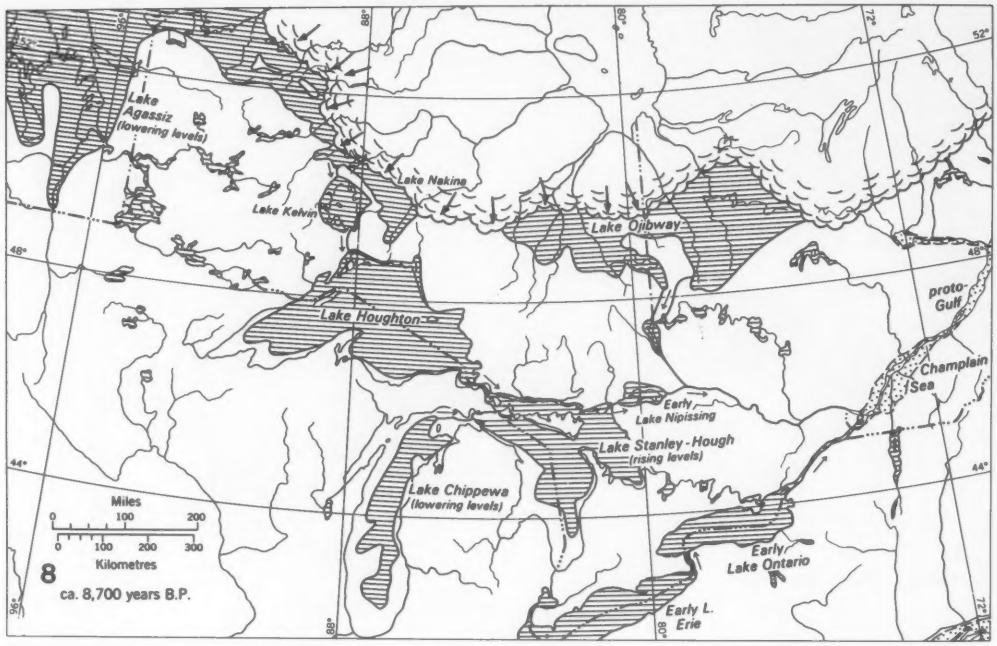
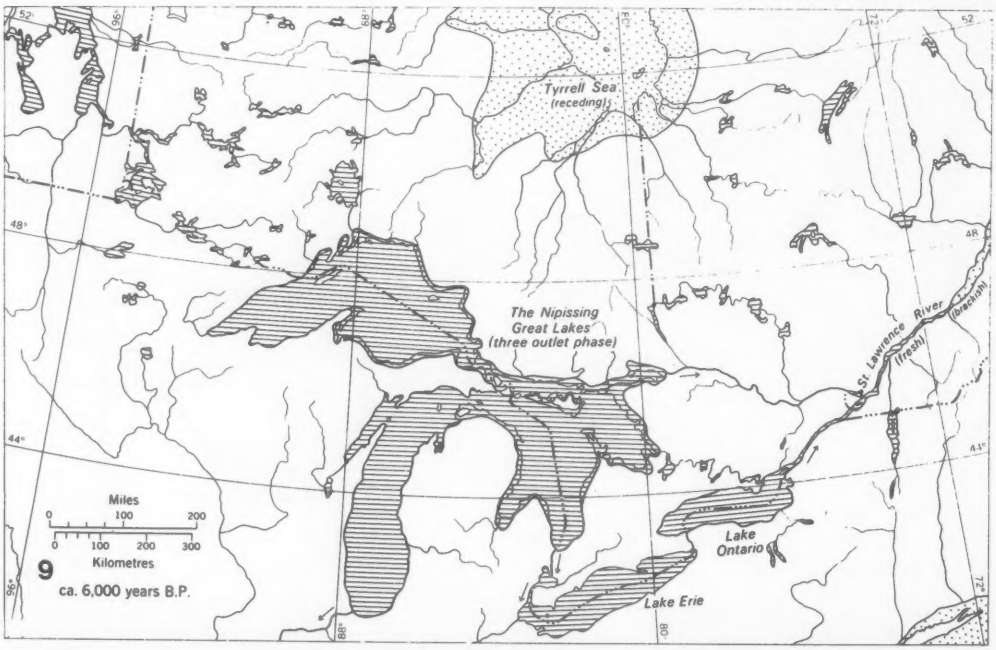


FIG. 6, 7. Lake Duluth, which appeared 11 600 yr ago, was the first zoogeographically significant lake in the Superior basin. At this time connections between Lake Agassiz and the Great Lakes were developing. By 10 300 yr ago crustal rebound was resulting in major separations among the basins. (From Prest 1970.)


Lake Agassiz (lowering levels)
Lake Kelvin
Lake Nakina
Lake Ojibway
Lake Houghton
proto-Gulf
Champlain Sea
Early Lake Nipissing
Lake Stanley-Hough (rising levels)
Lake Chippewa (lowering levels)
Early Lake Ontario
Early L. Erie
Miles
0 100 200
0 100 200 300
Kilometres
8
ca. 8,700 years B.P.


Tyrrell Sea (receding)
The Nipissing Great Lakes (three outlet phase)
St. Lawrence River (fresh)
(brackish)
Lake Ontario
Lake Erie
Miles
0 100 200
0 100 200 300
Kilometres
9
ca. 6,000 years B.P.

The Stage of Maximum Isolation of Numerous Lakes, 10 600–8100 Years Ago

At the end of the previous (Algonquin) stage lake habitat occupied and connected the Michigan, Huron, and western Superior basins. By 10 600 yr ago, dropping lake levels separated these basins except for fluvial connections. Lakes Erie and Ontario were not connected to Lake Algonquin at this time, but drained to the Champlain Sea. The upper lakes drained separately to the Champlain Sea through the North Bay outlet (Fig. 7).

Lake Ojibway–Barlow formed along the front of receding ice that covered Hudson Bay. This lake discharged into the river fed by the North Bay outlet, but was also connected to waters confluent with the Superior basin to the northwest. Various connections also existed between the Superior basin and Lake Agassiz 9500–8700 yr ago. Lake Kelvin, in the Nipigon basin, and Lake Nakina, tributary to Lake Kelvin from the east and northeast, provided dispersal routes among Ojibway–Barlow, Minong–Houghton (Superior basin), and Agassiz at this time (Fig. 8; Zoltai 1965, 1967a, b; Prest 1970).

It was during this period of broad connections in the north and relative restriction in the south that potential dispersal routes to and from the Arctic developed along the chain of large lakes that formed as the Laurentide ice sheet receded along a southeast–northwest line now occupied by Lake Winnipeg, Lake Athabaska, Great Slave Lake, and Great Bear Lake. Lake Agassiz transgressed over 200 000 square miles (500 000 km^2) of this area (noncontemporaneously) and had at least a brief outlet northwest to the Lake Athabaska area (Elson 1967, p. 39). The largest of the lakes in this chain, Lake McConnell, covered as much as 9° of latitude, spanning the area of Lake Athabaska to Great Bear Lake (Craig 1965). Continuity (possibly noncontemporaneous) of lacustrine habitat along this chain was significant for northward dispersal of many Great Lakes fishes.

The maximum separation among the Great Lakes and associated bodies of water occurred 10 500–8000 yr ago, but progressed unevenly. Eastern and western basins of Lake Superior might have been divided briefly 10 600 yr ago (Prest 1970, fig. 16m). Division of the Huron basin into three separate lakes associated with early Lake Nipissing and Lake Ojibway–Barlow existed 10 600–9000 yr ago (Fig. 7; Prest 1970). Two lakes occupied the Michigan basin 8400 yr ago. The Lampsilis Lake occupied the St. Lawrence Valley 8400–7400 yr ago. Lakes Nakina and Kelvin existed north of Lake Superior. Lake Kelvin drained to Lake Superior through the Black Sturgeon River 9500 yr ago (Zoltai 1965, p. 265). Lake Nakina afforded the last dispersal route into the Nipigon basin 9000–8700 yr ago (Fig. 8; Zoltai 1967b; Prest 1970). Lake Nipigon is now inaccessible from Lake Superior because of barrier falls near the source of the Nipigon River.

The Broadly Connected Stage (Approximately Nipissing), 8100–6000 Years Ago

Lake levels rose during the Nipissing stage in response to restriction of the North Bay outlet by crustal rebound. Most of the isolation seen in the previous stage was eliminated. The remnant of Lake Ojibway disappeared and the Tyrell Sea began the transition to Hudson Bay. Lake Agassiz receded to Lake Winnipeg. The North Bay outlet released diminishing flow to Lampsilis Lake in the St. Lawrence Valley. As waters rose in the Great Lakes, the Nipissing stage closed with an episode of maximum intercommunication among the Michigan, Huron, and Superior basins (Fig. 9) and Lake Huron finally began to discharge again through Lake St. Clair and Lake Erie. Reopening of the Chicago outlet to the Illinois River temporarily permitted the last major dispersal exchange with the Mississippi drainage. This stage, the Nipissing Great Lakes three-outlet phase, marks the last of the major dispersal connections of the premodern configuration of the lakes.

Modern Stage, 6000 Years Ago to the Present

Cessation of the Chicago and North Bay outlets brought about the modern isolation of the Great Lakes from the Mississippi drainage and the one-way isolation of the upper Great Lakes and Lake Erie from Lake Ontario (Fig. 1). The latter isolation was breached in 1825 by the Welland Canal, with far-reaching effects by dispersants. Were prehistoric connections equally important in admitting new forms to the fauna? The answer can only be sought by study of the patterns of fish distributions in relation to the time and place of known barriers and connections.

Summary: Chronology and Pattern of Barriers and Connections

1) Initial connection between the Michigan basin and the Illinois–Mississippi drainage 14 000–11 500 yr ago (Fig. 2–6).

2) Connection of the Huron and Erie basin to the Wabash–Ohio–Mississippi drainage 14 000 yr ago (Fig. 2).

3) Connection of the Ontario basin to the Susquehanna drainage 13 600–13 200 yr ago (Fig. 3) and perhaps later, see discussion below.

4) Connection of the St. Lawrence basin to the Hudson River drainage 13 600–12 000 yr ago (Fig. 3, 4).

5) Intermittent discharge of Lake Agassiz to the Red River–Mississippi drainage 12 800–10 000 yr ago (Fig. 4–6).

6) Direct discharge from the Huron basin to the Ontario basin 12 000 yr ago (Fig. 4).

7) Two fluvial connections between the Ontario and Hud-

FIG. 8, 9. Lakes Nakina and Kelvin, north of Lake Superior, provided major communication between Lake Agassiz and the Lake Superior basin 8700 yr ago. At this time Lake Ojibway was well developed and draining into the North Bay outlet. The Lake Michigan basin was approaching the stage in which northern and southern lakes were briefly separate (8400 yr ago). The Nipissing Great Lakes three-outlet phase provided maximum intercommunication among the lakes. External connection existed from Lake Michigan to the Mississippi. Drainage to the St. Lawrence occurred through the North Bay outlet as well as the lower lakes. (From Prest 1970.)

TABLE 2. Summary tabulation of Great Lakes Fishes[1] by lakes (see Table 3 for details).

	Lake Nipigon basin	Lake Superior	Lake Superior tributaries	Lake Michigan	Lake Michigan tributaries	Lake Huron	Lake Huron tributaries	Lake St. Clair, St. Clair River, Detroit River, and tributaries	Lake Erie	Lake Erie tributaries	Lake Ontario	Lake Ontario tributaries	Great Lakes basin
Total forms, native and alien	40	53	82	91	135	90	112	108	106	125	95	125	180
Native forms, living and extirpated	38	43	70	79	119	76	99	97	91	107	85	113	159
Native forms, probably or certainly extirpated in drainage	0	0	2	5	3	5	2	1	7	4	4	3	9
Alien species, introduced directly, colonized after introduction elsewhere, or through man-made access	2	10	12	12	16	14	13	11	15	18	10	12	21

[1]In this table no distinction is drawn between full species and subspecies as listed in Table 3. However, no subspecies of the Coregoninae or Cottidae are included.

son drainages 12 800–12 000 yr ago (Fig. 4; Prest 1970, fig. 16f).

8) First appearance of a permanent lake in the Superior basin 11 600 yr ago. Its drainage was temporarily to the Mississippi basin. Colonization of streams above the falls along the south shore of the lake had to occur at this time of high lake levels (Fig. 6).

9) Separation of the connection between the Huron and Erie basins 11 200–6000 yr ago (Fig. 7, 8).

10) Dispersal routes between the Great Lakes and Arctic drainage through Lake Agassiz and Lake McConnell about 10 300–8700 yr ago (Fig. 6–8).

11) Dispersal routes between the Superior basin (L. Houghton) and the Nipigon basin (L. Kelvin) 9500–8700 yr ago (Fig. 8).

12) Partial barriers (fluvial connections) between the Michigan, Huron, and Superior basins 10 600–8200 yr ago (Fig. 7, 8; Prest 1970, fig. 16m–t).

13) Final occurrences of the Chicago connection between Lake Michigan and the Mississippi basin, and of the North Bay outlet to the St. Lawrence, 6000 yr ago (Fig. 9). (Modern dredged waterways have reopened these channels.)

14) Beginning of the modern configuration of the Great Lakes 6000 yr ago (Fig. 1).

PALEOECOLOGY

Identified fossil fishes have not been reported from periglacial deposits of known age. Zoltai and Herrington (1966) report naiads (requiring fish hosts for the glochidial stage) and a small, unidentified fish jaw from early glaciolacustrine silts and clays from the area north of Lake Superior.

The most striking evidence for extensive fish habitat in the periglacial lakes comes indirectly from fossil whales and walruses (Handley 1953). A finback whale rib (*Balaenoptera*, Univ. Mich. Mus. Paleontol. 14101) from a Lake Arkona beach in Genesee County, Michigan, is evidence for a large aquatic habitat along the Grand River and Chicago outlets, as well as the Mississippi River. A vertebra and rib of a sperm whale (*Physeter*, UMMP 14102) from near Lake Whittlesey beach deposits in Lenawee County, Michigan, also implies a large discharge through the Grand River and Chicago outlets. A rib of a bowhead whale (*Balaena*, UMMP 11008) from 1.5 m below Nipissing deposits in Iosco County, Michigan, is evidence for large volume in the North Bay outlet to the St. Lawrence. Two fossil records of walruses from near the Straits of Mackinac provide similar evidence (Handley 1953). Later fish records from the Michigan and Huron basins indicate environments more like those of today. The fossils are recent species near their present ranges (Wilson 1967; Teller and Bardack 1975; Teller-Marshall and Bardack 1978; Hubbs 1940).

The previous discussion has been limited to the past 14 000 yr. Availability of lacustrine habitat during the long period of glacial advance was more restricted than during recessions because south of the Great Lakes basin the slope of the drainage is generally southward. Ice-dammed lakes were not common except in regions like the driftless area of Wisconsin and Illinois, which contained a large lake (Lake Wisconsin) (Flint et al. 1959). Such a lake would provide excellent habitat because it would be less turbid than periglacial lakes. Meltwater channels from the glaciers were occasionally large, but seasonal instability would not have favored a diversified fish fauna.

In summary, during the 70 thousand years of Wisconsinan glaciation, lake habitats for fishes would have been common in the periglacial zone only during glacial retreats. The problem of refugia for lake fishes during glacial advances is not

TABLE 3. Distribution of fishes in the Great Lakes basin: × = present, native; o = extirpated, formerly native; i = introduced; c = colonized recently via canal or by natural dispersal following introduction; ? = questionable or unverified report. Unsuccessful or temporary introductions are omitted. Records of species that are typically small-stream or bog inhabitants but that have been taken in bays or as stragglers in the main lakes are included; additional strays may be anticipated in the large lakes, especially near stream mouths. In the column for Lake Nipigon, tributary waters are included; in that for Lake St. Clair, the St. Clair and Detroit rivers and their tributaries are included.[a] Summary, Table 2.

	Distribution												Refuge and access route				
	L. Nipigon	L. Superior	Tributaries	L. Michigan	Tributaries	L. Huron	Tributaries	L. St. Clair and tributaries	L. Erie	Tributaries	L. Ontario	Tributaries	St. Croix	Fox	Chicago	Maumee	Atlantic
Petromyzontidae																	
Ichthyomyzon castaneus				×	×									×	×		
I. fossor			×		×		×	×		×				×	×	×	
I. unicuspis		×	×	×	×	×	×	×	×	×	×	×		×		×	
Lampetra appendix			×		×		×	×		×		×			×	×	
Petromyzon marinus		c	c	c	c	c	c	c	c	c	×	×					×
Polyodontidae																	
Polyodon spathula			o		o	o	o		o						×	×	
Acipenseridae																	
Acipenser fulvescens	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Lepisosteidae																	
Lepisosteus oculatus					×			×	×	×					×	×	
L. osseus		×	×	×	×	×	×	×	×	×	×	×		×	×	×	
L. platostomus				c	c									c			
Amiidae																	
Amia calva		×	×	×	×	×	×	×	×	×	×	×		×	×	×	
Anguillidae																	
Anguilla rostrata		c	c	c	c	c	c	?	c	c	×	×		c	c		×
Hiodontidae																	
Hiodon tergisus				×	×	×		×	×	×	×	×		×	×	×	
Clupeidae																	
Alosa pseudoharengus		c	c	c	c	c	c	c	c		i	c					
Dorosoma cepedianum		×		×	×	×	×	×	×	×	×	×			×	×	
Salmonidae																	
Salmoninae																	
Oncorhynchus gorbuscha		c	i	c	c	c	c	c	c	c	c	c					
O. kisutch		i	i	i	i	i	i	i	i	i	i	i					
O. nerka						i	i										
O. tshawytscha		i	i	i	i	i	i	i	i	i	i	i					
Salmo gairdneri		i	i	i	i	i	i	i	i	i	i	i					
S. salar				i		i					o	o					×
S. trutta		i	i	i	i	i	i	i	i	i	i	i					
Salvelinus fontinalis	×	×	×	×	×	×	×	i		i		×			×		×
S. namaycush	×	×	×	×	×	×	×	×	×		×	×			×	×	×
Thymallinae																	
Thymallus arcticus			o		o		o								×	×	
Coregoninae[a]																	
Coregonus artedii	×	×	×	×	×	×	×	×	×	×	×	×		×	×	×	
C. hoyi	×	×		×	×	×					×			Endemic			
C. johannae				o		o								Endemic			
C. kiyi		×		o		o					o			Endemic			
C. nigripinnis	×			o		o								Endemic			
C. reighardi				o		×					o			Endemic			
C. zenithicus	×	×	×	o		o			o						×	×	
C. clupeaformis	×	×	×	×	×	×	×	×	×	×	×	×			×	×	×
Prosopium coulteri		×													×	×	
P. cylindraceum	×	×	×	×		×	×				×	×			?		×
Osmeridae																	
Osmerus mordax		c	c	c	i	c	c	c	c	c	c	c					
Umbridae																	
Umbra limi			×	×	×	×	×	×	×	×	×	×	×	×	×	×	

TABLE 3. (*Continued*)

	Distribution												Refuge and access route				
	L. Nipigon	L. Superior	Tributaries	L. Michigan	Tributaries	L. Huron	Tributaries	L. St. Clair and tributaries	L. Erie	Tributaries	L. Ontario	Tributaries	St. Croix	Fox	Chicago	Maumee	Atlantic
Esocidae																	
Esox americanus vermiculatus				×	×		×	×	×	×	×	×			×	×	
E. lucius	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
E. masquinongy		×	×	×	×	×	×	×	×	×	×	×		×	×	×	
E. niger											×	×					×
Cyprinidae																	
Campostoma anomalum					×		×	×	×	×	×	×		×	×	×	
C. oligolepis					×									×	×		
Carassius auratus				i	i	i	i	i	i	i	i	i					
Couesius plumbeus	×	×	×	×	×	×	×				×	×			×	×	×
Cyprinus carpio		i	i	i	i	i	i	i	i	i	i	i					
Ericymba buccata					×				×	×					×	×	
Exoglossum laurae												×[b]					
E. maxillingua												×					×
Hybognathus hankinsoni			×		×		×	×		×		×		×	×	×	
H. regius											×	×					×
Hybopsis amblops					?			×		×		×				×	
H. storeriana								×	×	×		×				×	
H. x-punctata								×								×	
Nocomis biguttatus			×		×		×	×		×	×	×	×	×	×	×	
N. micropogon					×		×	×		×		×				×	
Notemigonus crysoleucas		×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Notropis analostanus												×					×
N. anogenus					×		×	×	o	×		×		×	×	×	
N. ariommus										o						×	
N. atherinoides	×	×	×	×	×	×	×	×	×	×	×	×		×	×	×	
N. bifrenatus											×	×					×
N. blennius					×									×			
N. boops										o						×	
N. buchanani								×							×		
N. chalybaeus					×									×	×		
N. chrysocephalus				×	×		×	×	×	×	×	×			×	×	
N. cornutus			×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
N. dorsalis			×		×					×		×	×	×	×	×	
N. emiliae					×			×	×	×				×	×	×	
N. heterodon			×	×	×		×	×	o	×	×			×	×	×	
N. heterolepis	×	×	×	×	×	×	×	×	o	×		×	×	×	×	×	
N. hudsonius	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
N. photogenis										×						×	
N. procne												c					×
N. rubellus			×	×	×	×	×	×	×	×	×	×		×	×	×	
N. spilopterus				×	×	×	×	×	×	×	×	×		×	×	×	
N. stramineus			×	×	×	×	×	×	×	×	×	×	×	×	×	×	
N. texanus					×		×							×	×		
N. umbratilis					×		×	×		×		×		×	×	×	
N. volucellus	×		×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Phenacobius mirabilis										c						×	
Phoxinus eos	×		×	×	×	×	×	×		×		×	×	×	×	×	
P. erythrogaster					×					×				×	×	×	
P. neogaeus	×		×		×		×	o				×		×	×	×	
Pimephales notatus			×	×	×	×	×	×	×	×	×	×	×	×	×	×	
P. promelas	×		×	×	×	×	×	×	×	×	×	×	×	×	×	×	
P. vigilax perspicuus					×					c				×		×	
Rhinichthys a. atratulus												×					×
R. atratulus meleagris			×	×	×		×	×	×	×		×	×	×	×	×	
R. cataractae	×	×	×	×	×	×	×		×	×	×	×	×	×	×	×	×

TABLE 3. *(Continued)*

	Distribution												Refuge and access route				
	L. Nipigon	L. Superior	Tributaries	L. Michigan	Tributaries	L. Huron	Tributaries	L. St. Clair and tributaries	L. Erie	Tributaries	L. Ontario	Tributaries	St. Croix	Fox	Chicago	Maumee	Atlantic
Richardsonius elongatus					×			×		×		×		×	×	×	
Semotilus atromaculatus			×	×	×		×	×	×	×	×	×	×	×	×	×	×
S. corporalis											×	×					×
S. margarita margarita												×					×
S. m. nachtriebi	×		×	×	×		×	×		×	×	×	×	×	×	×	
Catostomidae																	
Carpiodes cyprinus				×	×	×	×	×	×	×	×	×		×	×	×	
Catostomus catostomus	×	×	×	×	×	×	×		×		×	×			×	×	×
C. commersoni	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Erimyzon oblongus claviformis					×					×					×	×	
E. o. oblongus												×					×
E. sucetta					×	×	×	×	×	×		×		×	×	×	
Hypentelium nigricans					×	×	×	×	×	×	×	×		×	×	×	
Ictiobus cyprinellus					×			×	×	×				×	×	×	
I. niger					×	i			i						×		
Lagochila lacera										o						×	
Minytrema melanops					×		×	×	×	×				×	×	×	
Moxostoma anisurum	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
M. carinatum					×		×	×		×					×	×	
M. duquesnei					×		×	×	×	×		×			×	×	
M. erythrurum				×	×		×	×	×	×		×		×	×	×	
M. macrolepidotum	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
M. valenciennesi				×	×	×	×	×	×	×	×	×		×	×	×	
Cobitidae																	
Misgurnus anguillicaudatus							i										
Ictaluridae																	
Ictalurus catus									i	i							
I. melas			×	×	×	×	×	×	×	×	×	×		×	×	×	
I. natalis			×	×	×	×	×	×	×	×	×	×		×	×	×	
I. nebulosus		×	×	×	×	×	×	×	×	×	×	×		×	×	×	×
I. punctatus			×	×	×	×	×	×	×	×	×	×		×	×	×	
Noturus flavus			×		×	×	×	×	×	×	×	×	×	×	×	×	
N. gyrinus			×		×	×	×	×	×	×	×	×	×	×	×	×	
N. insignis			i									×					×
N. miurus								×	×	×		×				×	
N. stigmosus								×		×						×	
Pylodictis olivaris					×				×	×				×	×	×	
Aphredoderidae																	
Aphredoderus sayanus					×		×		?	×		×		×	×	×	
Percopsidae																	
Percopsis omiscomaycus	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Gadidae																	
Lota lota	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Cyprinodontidae																	
Fundulus d. diaphanus											×	×					×
Fundulus d. menona			×	×	×	×	×	×	×	×	×	×		×	×	×	
F. dispar dispar					×										×		
F. notatus					×					×				×	×	×	
Poeciliidae																	
Gambusia affinis					i					i							
Atherinidae																	
Labidesthes sicculus			i	×	×		×	×	×	×	×	×		×	×	×	
Gasterosteidae																	
Culaea inconstans	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Gasterosteus aculeatus											×	×					×
Pungitius pungitius	×	×	×	×	×	×	×	×			×	×			×	×	×

TABLE 3. (*Concluded*)

	Distribution												Refuge and access route				
	L. Nipigon	L. Superior	Tributaries	L. Michigan	Tributaries	L. Huron	Tributaries	L. St. Clair and tributaries	L. Erie	Tributaries	L. Ontario	Tributaries	St. Croix	Fox	Chicago	Maumee	Atlantic
Percichthyidae																	
Morone americana									c		c	c					×
M. chrysops		×		×	×	×	×	×	×	×	×	×		×	×	×	
M. mississippiensis					i												
Centrarchidae																	
Ambloplites rupestris		×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Enneacanthus gloriosus												i					
Lepomis cyanellus					×		×	×	×	×		×		×	×	×	
L. gibbosus			×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
L. gulosus					×		×		×	×					×	×	
L. humilis									c	c						×	
L. macrochirus			×	×	×	×	×	×	×	×	×	×		×	×	×	
L. megalotis peltastes					×	×	×	×	o	×		×		×	×	×	
L. microlophus					i					i							
Micropterus dolomieui	i		×	×	×	×	×	×	×	×	×	×	×	×	×	×	
M. salmoides			×	×	×	×	×	×	×	×	×	×		×	×	×	
Pomoxis annularis				×	×	×	×	×	×	×	×	×			×	×	
P. nigromaculatus	i		×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Percidae																	
Ammocrypta clara					×									×			
A. pellucida							×	×	×	×						×	
Etheostoma blennioides					×		×	×	×	×		× [c]				×	
E. caeruleum					×		×	×		×		×		×	×	×	
E. chlorosomum					o										×		
E. exile	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
E. f. flabellare					×		×	×	×	×	×	×				×	
E. f. lineolatum				×	×									×			
E. microperca			×		×		×	×		×		×	×	×	×	×	
E. nigrum	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
E. olmstedi											×	×					×
E. spectabile										×						×	
E. zonale					×									×			
Perca flavescens	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Percina caprodes	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
P. copelandi						×	×	×	×	×		×				×	
P. evides										o						×	
P. maculata			×		×		×	×	×	×		×		×	×	×	
P. phoxocephala					×									×			
P. shumardi					c	×	×	×	×	×				×		×	
Stizostedion canadense	×	×	×	×	×	×	×	×	×	×	×	×		×	×	×	
S. vitreum glaucum									o		o	o		Endemic			
S. v. vitreum	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
Sciaenidae																	
Aplodinotus grunniens				×	×	×	×	×	×	×	×	×		×	×	×	
Cottidae																	
Cottus bairdi	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
C. cognatus	×	×	×	×	×	×	×	×	×		×	×	×	×	×	×	×
C. ricei	×	×	×	×	×	×	×		×		×				×	×	
Myoxocephalus thompsoni	×	×		×		×			×		×			×	×	×	

completely solved. All data indicate that stream habitats were more stable, notwithstanding the north–south shifts.

Glacial Refugia and Postglacial Dispersal

It has been widely assumed that several Great Lakes fish species dispersed from the northwest during deglaciation. Radforth (1944) and Hubbs and Lagler (1958) cited *Salvelinus namaycush*, ciscoes (*Coregonus* spp.), *Percopsis omiscomaycus*, *Myoxocephalus* (*thompsoni*), *Cottus cognatus*, and *Cottus ricei* as examples. However, McPhail and Lindsey (1970) presented evidence that *Coregonus artedii* and *Percopsis omiscomaycus* dispersed northward from the Mississippi drainage, where each is represented by living populations, and that *Coregonus clupeaformis* and *Cottus ricei* also dispersed from the upper Mississippi valley. These authors also provided evidence that 13 Great Lakes species, including *Prosopium cylindraceum*, *P. coulteri*, *Thymallus arcticus*, *Salvelinus namaycush*, *Myoxocephalus* (*thompsoni*), and *Cottus cognatus*, survived the glaciation in the Mississippi as well as other North American refuges. Other Great Lakes species in this category, according to McPhail and Lindsey, are *Esox lucius*, *Couesius plumbeus*, *Rhinichthys cataractae*, *Catostomus catostomus*, *Lota lota*, *Pungitius pungitius*, and *Gasterosteus aculeatus*. Our explanation of the distributional evidence is in agreement with the conclusions of McPhail and Lindsey, except that we believe that *Prosopium cylindraceum* entered the Great Lakes basin from an Atlantic rather than a Mississippi refugium. We interpret no Great Lakes species as a colonist from the northwest during deglaciation. Most Great Lakes species were evidently a part of the Mississippi basin fauna during Wisconsinan glaciation, but a substantial fraction of the fauna probably inhabited tributaries along the Atlantic coast.

The Bering Refugium

The widespread occurrence in unglaciated Bering drainages of *Salvelinus namaycush*, *Thymallus arcticus*, the *Coregonus clupeaformis* complex, *Prosopium cylindraceum*, *Esox lucius*, *Catostomus catostomus*, *Lota lota*, *Pungitius pungitius*, and *Cottus cognatus* suggests that these species survived there during the Wisconsinan glacial stage. Walters (1955) believed that absence of *S. namaycush* from the eastern tip of Siberia cast doubt on its presence in the Bering refuge during glaciation, but Lindsey (1964) presented evidence for multiple refuges, including Beringia, for lake trout. McPhail and Lindsey argued that *Gasterosteus aculeatus* is a postglacial colonist of the Bering refuge because its distribution is limited to the southern part of the area, whereas eastern populations have greatly expanded their range northward (Scott and Crossman 1973, p. 666). *Myoxocephalus thompsoni* is generally regarded as a Pleistocene glacial relict in North America, but *Myoxocephalus* inhabited western North American lakes long before the Pleistocene (Smith 1975).

Along the southern shore of Lake Superior are streams with barrier falls separating *Esox masquinongy* (above the falls) and *Esox lucius* (below). *Esox lucius* has been observed to outcompete *E. masquinongy* in small habitats (Scott and Crossman 1973, p. 368). Its restriction below the falls indicates that it gained access to the drainage later than other species, after the ice had left the region. Yet *E. lucius* is more cold tolerant than *E. masquinongy*, and if it had been in the Mississippi basin during deglaciation it should have inhabited waters closer to the ice. Northern pike are vagile, opportunistic fish with the ability to survive in a variety of habitats. Diana et al. (1977) radiotracked pike as far as 4 km in 1 d and 10 km in 1 mo. Pike are not native to the upper Missouri drainage; along the Atlantic coast, they are native only to the St. Lawrence drainage. Fossil occurrences indicate that the muskellunge lineage has been in North American since the Miocene, but fossil pike are restricted to the Holocene, except in the Yukon (Crossman and Harington 1970; Teller and Bardack 1975). It is possible that pike colonized the Great Lakes from the northwest during deglaciation, through Lakes McConnell, Agassiz, and Nipigon. However, some evidence counter to this hypothesis exists in the differentiation of northern and southern Canadian populations, which suggests mul-

[a]*Footnote to Table 3*: For the species of *Coregonus* the entries follow Koelz (1929) with the following modifications (see also text p. 1556): *C. nigripinnis* is excluded from Lakes Ontario and Superior (occurrence in Lake Ontario is based on the type specimens of *C. prognathus* Smith, 1894, the status of which is uncertain (Todd 1981a); the Lake Superior stock is believed to be specifically identical with *C. zenithicus* (Todd and Smith 1980)); *C. nipigon* is regarded as a synonym of *C. artedii*, following Scott and Crossman (1973), as is *C. hubbsi* (Koelz), another variant form with relatively high gill-raker count from Ives Lake, Michigan; *C. bartletti* (Koelz) from Siskiwit Lake, Isle Royale, is considered to be *C. zenithicus*; *C. reighardi* is added to the Lake Huron faunal list, but populations of *C. r. dymondi* in Lakes Nipigon and Superior are interpreted as stocks of *C. zenithicus*; *C. alpenae* from Lakes Michigan and Huron, now extirpated, is treated as conspecific with *C. zenithicus* (R. M. V. Clarke and T. N. Todd in Lee 1980, p. 91); the extirpated stock of "*alpenae*" from Lake Erie was described by Scott and Smith (1961) but its status remains a question (it was identified with *C. johannae* by Hubbs and Lagler (1958)). Records given in this table are derived from a variety of sources including state and regional ichthyologies, studies of individual lake faunas, systematic lists and monographs, and specimens in the Museum of Zoology of the University of Michigan. Some published reports that are viewed as highly dubious or as based on misidentified or mislabeled specimens have been excluded or are indicated by question marks. Most but probably not all of the literature source works are listed in the bibliography. We do not attempt individual documentation for all records. Nomenclature with few exceptions follows Robins et al. (1980), where authorities are given for all species.

[b]For explanation of dispersal of *Exoglossum laurae* see text p. 1554.

[c]For explanation of dispersal of *Etheostoma blennioides* see text p. 1554.

tiple refugia for pike (McPhail and Lindsey 1970; Morrow 1980).

The Atlantic Refugia

Thirty-six species colonized the Great Lakes from Atlantic drainage refugia (Table 3). Fourteen species (17 kinds) of these entered only from the Atlantic, 22 species from both Atlantic and Mississippi refugia. Differentiated forms of *Rhinichthys atratulus*, *Semotilus margarita*, *Erimyzon oblongus*, *Fundulus diaphanus*, and possibly *Cottus bairdi* entered from dual refugia.

The following species of management interest had populations in the Atlantic refugia; some of these might be expected to show significant differentiation of eastern and western stocks: *Petromyzon marinus*, *Salmo salar*, *Salvelinus fontinalis*, *Salvelinus namaycush*, *Coregonus clupeaformis*, *Prosopium cylindraceum*, *Esox niger*, *Anguilla rostrata*, *Catostomus catostomus*, *Catostomus commersoni*, *Ictalurus nebulosus*, *Lota lota*, *Lepomis gibbosus*, and *Perca flavescens*.

The Mississippi Refugia

Most species of Great Lakes fishes must have inhabited the Mississippi headwaters during glaciation. The western drainages near the Missouri, the upper Mississippi, the Illinois, Wabash, and Ohio drainages were probably refugia during much of the period. During the later stages of deglaciation the main southern points of entry into the Great Lakes were the Chicago outlet (Fig. 3–5, 9), the Maumee outlet from Lake Maumee (Erie basin) to the Wabash 14 000 yr ago, the outlets from Lake Duluth (Superior basin) to the Mississippi 11 500 yr ago (Greene 1935, p. 13), and the seasonal Fox River portage between the Wisconsin River and Green Bay of Lake Michigan. Canals have since increased the number of access routes from the south (Hubbs and Lagler 1958). Most of the 134 species that entered from Mississippi refugia are tributary inhabitants, and are generally small forms of little economic importance. Those of management interest include *Acipenser fulvescens*, 3 species of gars, *Hiodon tergisus*, *Dorosoma cepedianum*, *Salvelinus fontinalis*, *Salvelinus namaycush*, *Thymallus arcticus*, *Coregonus clupeaformis*, *Coregonus artedii* and related stocks (see below), *Esox lucius*, *Esox masquinongy*, about 10 species of suckers, *Ictalurus punctatus*, 3 species of bullheads (*Ictalurus*), *Pylodictis olivaris*, *Lota lota*, *Morone chrysops*, 9 kinds of bass and sunfish, *Perca flavescens*, *Stizostedion vitreum*, *Stizostedion canadense*, and *Aplodinotus grunniens*. The 17 species that also entered from Atlantic refugia (Table 3) are most likely to display genetic differentiation.

In the Great Lakes watershed *Exoglossum laurae* is restricted to the southern part of the Genesee River above the barrier falls at Portageville, Wyoming County, New York. Otherwise that species is confined to the Ohio River basin where it has a disjunct distribution in three areas, of which only that in the upper Allegheny River basin is in proximity to the Great Lakes basin (Raney 1941; R. E. Jenkins, C. R. Gilbert, and S. H. Taub in Lee et al. 1980, p. 157). Raney commented that the species "most likely ... reached the Genesee from the Allegheny system by utilizing postglacial outlets." Stream capture provides a probable explanation. A low valley crosses the watershed in western Allegany County, New York, between the villages of North Cuba and Black Creek. This valley is traversed by a railroad and by Highway 305 between Olean and Belfast. Oil Creek flows south through Cuba Lake Reservoir, enters the valley at North Cuba, and flows southwest into Olean Creek and the Allegheny River. The barbed, upper part of Black Creek flows into the valley at a point about 3 km northeast of North Cuba and flows northeast to join the Genesee near Belfast, well above the impassable falls at Portageville. The geological evidence indicates that the barbed upper part of Black Creek formerly flowed into Oil Creek which was beheaded and diverted by headward erosion of Black Creek. Zoogeographic support for this interpretation is provided by a fish collection taken in Oil Creek near Scott, about 12 km below the point of diversion, on July 28, 1937, by a New York Conservation Department Survey party consisting of J. R. Greeley, P. W. Gilbert, and R. M. Bailey. Fishes taken (deposited in the University of Michigan Museum of Zoology) include, significantly, *Exoglossum laurae* and 19 other species. Among these, *Notropis photogenis* and *Etheostoma zonale* are unknown in the Ontario watershed, and *Nocomis micropogon*, *Notropis volucellus*, and *Etheostoma caeruleum* are absent from the upper part of the Genesee basin. If involved in the diversion, these species were apparently unsuccessful. *Etheostoma b. blennioides* also successfully entered the upper Genesee from the Allegheny (Miller 1968) where it is present above Portageville Falls; the lower Genesee was populated from the west by a different stock, *E. b. pholidotum*, that is rare elsewhere in the Ontario watershed. Most of the other species taken are common in both drainages and offer no evidence on the transfer. The stock of *Percina caprodes* in the upper Genesee should be compared with Ohio basin and Lake Ontario stocks which are currently assigned to different subspecies. *Semotilus m. margarita*, not represented in the Oil Creek collection, is nevertheless common in headwater streams in the Allegheny drainage and it too may have been involved in the stream capture. Dr C. Lavett Smith has called our attention to the fact that the old Genesee Canal utilized the same route as the stream capture described above. Thus, entry of Allegheny species into the upper Genesee may date from an early stream capture, a more recent canal connection, or both. The observation by Miller (1968, p. 33) of some differentiation between the populations of *E. b. blennioides* in these areas following isolation suggests that the older connection is the more likely.

An additional point of entry of fishes from the western part of the Mississippi drainage is the connection from Lake Agassiz through Pleistocene Lakes Kelvin and Nakina. Lake Agassiz was a potential source of upper Mississippi forms, which might have differentiated in the west at least 12 900–8700 yr ago, and possibly earlier. Their access to the Great Lakes occurred 10 900–8700 yr ago (e.g. Fig. 7). These fishes, especially *Salvelinus namaycush* and stocks of *Coregonus*, are probably the basis of some of the genetic diversity in the western basins.

Subspecies

In our tabulation of 174 species of Great Lakes fishes, 6 are treated as containing two subspecies each. In contrast, Hubbs

and Lagler (1958, p. 11) listed 173 species and 234 total forms including subspecies. Much of the difference reflects their provisional acceptance of 14 species and 45 total taxa among the coregonines, in contrast with our conservative listing of 10 species and no additional subspecies. Beyond that, however, they have accepted two or more subspecies for other species in which we believe that present data do not warrant subspecific partition in the Great Lakes area (e.g. *Salmo salar*, *Salvelinus namaycush*, *Carpiodes cyprinus*, *Catostomus catostomus*, *Catostomus commersoni*, *Notemigonus crysoleucas*, *Notropis atherinoides*, *N. dorsalis*, *N. heterolepis*, *N. hudsonius*, *N. stramineus*, *Pimephales promelas*, *Esox masquinongy*, *Gambusia affinis*, and *Etheostoma nigrum*). For a few species (i.e. *Campostoma anomalum*, *Couesius plumbeus*, *Percina caprodes*, and *Cottus bairdi*) we have utilized binomials provisionally because the status of subspecies is unclear. These are currently under study by others.

During Wisconsinan glaciation at least four species occupied western and eastern refugia from which the separated stocks utilized postglacial channels to invade the Great Lakes. In each species differentiation is well marked, permitting essentially complete separation of individuals. *Rhinichthys a. atratulus* invaded the Lake Ontario basin from the east, occupying small streams as far west as Wolcott in Wayne County, New York. *Rhinichthys a. meleagris*, spreading from a Mississippi refugium, attained an eastern limit in Mudge Creek west of Wolcott; thus the two forms have complementary distributions, show no evidence of intergradation, and may prove to be better regarded as species than as subspecies (Greeley 1940, p. 73). In a similar pattern of occupation, *Fundulus diaphanus menona*, which occurs in typical form above Niagara Falls, met *F. d. diaphanus*,' the Atlantic slope form, the two intergrading in the Lake Ontario basin. Fish from the western part of the area closely approach *menona* and grade clinally into near typical *diaphanus* eastward (Shapiro 1947; C. R. Gilbert and J. R. Shute in Lee et al. 1980, p. 513). Subspecies of the chubsucker *Erimyzon oblongus* entered the southern part of the Lake Ontario basin from an Atlantic refugium (*E. o. oblongus*) and the southern parts of the Lake Michigan and Lake Erie drainages from a Mississippi refugium (*E. o. claviformis*). In the Great Lakes they are widely separated (B. R. Wall Jr. and C. R. Gilbert in Lee et al. 1980, p. 398), but the subspecies intergrade in Georgia. Two subspecies of the pearl dace, *Semotilus margarita*, occur in the Lake Ontario basin. The wide-ranging *S. m. nachtriebi*, including the nominal *S. m. koelzi* from Harvey Lake, Isle Royale, is distributed from Northwest Territories and British Columbia to Quebec and Nova Scotia, and lives in much of Ontario and northern New York. It evidently entered the Great Lakes from a Mississippi basin refugium. *Semotilus m. margarita* has a restricted distribution on the Atlantic slope from Virginia to southern New York and in the upper Allegheny system. Either or both areas probably served as glacial refugia, with postglacial entry into the Genesee (see p. 1554) and Oswego river basins (Greeley 1940, p. 97–98) by stream capture or other headwater connections. The subspecies are well differentiated, are not known to occur together, and when thoroughly studied may prove to be specifically distinct.

Two easily distinguished subspecies of the fantail darter, *Etheostoma flabellare*, apparently with discrete glacial refugia in the Mississippi basin, have invaded the Great Lakes basin. *Etheostoma f. flabellare* entered through the Wabash–Maumee portal and has dispersed from eastern lower Michigan to the Lake Michigan drainage of Michigan and east through the lower Great Lakes to Quebec. An upper Allegheny population may also have crossed by stream capture into the Genesee drainage of the Lake Ontario basin (p. 1554). To the west *E. f. lineolatum* utilized the Wisconsin–Fox outlet and now occupies western tributaries to Lake Michigan in Wisconsin and Michigan. The subspecies do not coexist in the Great Lakes basin (D. S. Lee in Lee et al. 1980, p. 647). As recorded above (p. 1554), Miller (1968) reported the entry of *Etheostoma b. blennioides* into the upper Genesee drainage of the Lake Ontario watershed from an upper Ohio basin refugium, and that of *E. b. pholidotum* via the Wabash–Maumee waterway into the lower Great Lakes.

The last and much the best known pair of subspecies in the Great Lakes system includes the widespread walleye, *Stizostedion v. vitreum*, and the now extinct blue pike, *S. v. glaucum*, formerly abundant in Lake Erie and common in Lake Ontario. The blue pike was endemic to these two lakes and presumably evolved there postglacially or in periglacial lakes. Alternatively, the stock may have been resident in a Mississippi refugium, invaded the Great Lakes, and then been extirpated from its refugium. With the exception of coregonines, the blue pike is the only endemic fish taxon in the Great Lakes basin. However, the distinctive copper redhorse, *Moxostoma hubbsi*, is endemic to the St. Lawrence drainage in Quebec (R. E. Jenkins in Lee et al. 1980, p. 424). It is hypothesized that *M. hubbsi* has been extirpated from a Mississippi glacial refugium, a prediction that awaits paleontological confirmation. The blue pike is distinguished from the walleye chiefly by its axanthic (blue) color, skull characters, and vertebral count. It was ranked as a species by some workers, but we contend that it is a stock of the walleye not appropriately accorded subspecific status if subspecies are defined as allopatric.

The *Coregonus* Problem

The most perplexing problem in understanding Great Lakes fish evolution concerns the origin and speciation of ciscoes and chubs of the genus *Coregonus*. Forty species and subspecies have been recognized in the Great Lakes area. We do not here address concern with the majority of these, mostly established by Koelz (1931) for allopatric, small inland-lake populations ranked by him as subspecies, 24 of *Leucichthys artedii* and 7 of *Coregonus clupeaformis*. Few workers have accorded recognition to these since the revelation by Hile (1937) and Svärdson (1950) of the notable interplay of the environment and development of morphometry and meristics in coregonines. Most of the taxa ranked as species (Koelz 1929, 1931), however, live in or closely adjacent to (e.g. *bartletti* and *hubbsi*) the Great Lakes and these, together with Great Lakes subspecies (Koelz 1929), have customarily been accepted by subsequent workers. The status of some of these taxa is questionable and the processes by which they diverged and dispersed are unknown. In this discussion we summarize our understanding of the characteristics of these fishes in relation to the hypothesis that only two species of *Coregonus*,

artedii and *clupeaformis*, are present in the Great Lakes basin.

The species-level classification of ciscoes and chubs has never been wholly satisfactory. When Walter Koelz began his studies on the group 60 yr ago, he encountered many invalid species recognized by other workers and much undescribed variation. Koelz (1929, p. 328) observed that "... the species of *Leucichthys* ... have hardly any other character than gill rakers by which the species, wherever they may occur, may be separated. Within a lake a few other characters may be of use to distinguish one or two species from the rest ..., but even these are not very constant, and each taken alone certainly could not be relied upon." Our investigations lead us to agree with the quoted statement. Koelz's descriptions are more accurate and complete than any others, and will probably remain so. However, the acknowledged lack of characters that completely separate these forms suggests that they may be locally distinct stocks or groups of stocks rather than species.

In practice, ichthyologists have regarded sympatric and modally distinct populations as separate species, based on the assumption that the distinguishing characters are either (1) incompletely evolved or (2) not yet discovered. Assumption (1), although convenient, is contradictory and not wholly defensible in our opinion. Assumption (2) has not been exhaustively challenged, but the search for species characters has been the object of considerable research.

A survey of isozymes (T. N. Todd, R. K. Koehn, and G. R. Smith, unpublished data; Todd 1981b) revealed relative homogeneity among *artedii*, *zenithicus*, *hoyi*, and *kiyi* of Lake Superior. Heterogeneity within groups is roughly equivalent to that between groups. A search for immunological and biochemical characters (Chellevold 1970) demonstrated similar homogeneity. Booke (1968, 1970) demonstrated differences in arm numbers among chromosomes of the ciscoes. The largest differences were between *artedii* and *hoyi*, the presumed parents of recently captured intermediate specimens from Lake Michigan. The 2*N* number is 80 for all forms, and little or no reproductive isolation is indicated. Study of certain species pairs and population groups suggests that *alpenae* and *zenithicus* are not specifically different (T. N. Todd and S. H. Smith, unpublished data) and that *zenithicus*, *reighardi dymondi*, and *nigripinnis cyanopterus* of Lake Superior are members of a polymorphic species complex (Todd and Smith 1980). Analyses of environmental influences on characters also lead to the conclusion that many named taxa may be based largely on environmentally induced variation (Hile 1937; Svärdson 1950; Todd et al. 1981), although genetic differences among stocks are clearly demonstrable (Todd 1981b).

Finally, our unpublished study of osteological characters suggests that *nigripinnis*, *nipigon*, and *hubbsi* are not different from *artedii*; *alpenae*, *bartletti*, *reighardi dymondi*, *nigripinnis cyanopterus*, and perhaps *johannae* are not different from *zenithicus*; and *hoyi* and *kiyi* are not different from each other. These three groups have distinguishing characters, but there is overlap among groups.

Koelz (1929) showed that between-lake variation in *kiyi*, *reighardi*, *nigripinnis*, and *artedii* is often more pronounced than some between-species variation within lakes. Smith (1964) and Todd and Smith (1980) cite similar evidence and interpretations. The problem persists that no character or combination of characters fully separate any of the species. We conclude that there is evidence in favor of recognizing fewer species, a conclusion arrived at independently by Clarke (1973).

To the contrary stand the monumental contributions of Koelz, whose abundant data and thorough analysis demonstrated sympatric kinds and led him to the alternate and generally accepted conclusion, which he still defends with enthusiasm (W. Koelz, personal communication, 1980). Furthermore, the species names assigned to the morphotypes that existed in the Great Lakes have been convenient for monitoring, managing, and understanding their diversity. The species names have called attention to this diversity in a way that would not have occurred otherwise. However, the level of classification affects the concept of the resource: if local stocks were managed as units for which extinction was permanent loss of a unique gene pool, rather than depletion of a small part of one of many widespread species, the loss would be seen as irreversible. We suggest that management will be more effective if based on the recognition that stocks may be especially vulnerable for an additional biological reason discussed below.

Biogeography of *Coregonus*

The most direct evidence for past distribution of these fishes is in the pattern of discontinuities in morphology, biochemical characters, and present distribution. *Coregonus clupeaformis* is represented by a similar form in the Bering Sea area (*C. pidschian*) with fewer gill rakers (Lindsey et al. 1970). The intermediate *C. nelsoni* suggests a zone of secondary contact in parts of Alaska (McPhail and Lindsey 1970; Morrow 1980). This is contraindicated, however, by biochemical evidence (Franzin and Clayton 1977) that lake whitefish from the south failed to enter Beringia, but that there was some eastward gene flow from the Yukon into northwestern and central Canada, where mixing with emigrants from a Mississippi refugium occurred. It seems probable that Great Lakes stocks were derived postglacially only from Mississippi and Atlantic refugia. Sympatric stocks or "sibling species" of the *clupeaformis* complex that differ in growth characteristics and gill-raker numbers have been reported and discussed for several well-separated North American lakes (e.g. Kennedy 1943; Fenderson 1964; Lindsey et al. 1970; Kirkpatrick and Selander 1979). Similar pairs of other fishes, mostly but not exclusively salmonoids, are known from many lakes in North America and Europe. In the lake whitefish, Lindsey et al. (1970) failed to find taxonomic equivalence between members of the sympatric pairs in different regions. They noted geographic differences in isozyme mobilities, but no consistency between geographic variation in the three isozymes studied. These authors believed that pair formation in Yukon Territory (Squanga Lake) and in the Atlantic region (Lake Opeongo, Ontario, and a group of adjacent lakes in Maine) were independent phenomena, a single form giving rise to two in the separate areas. The isozyme characteristics within each sympatric pair were identical or similar, but that the populations making up each pair constituted two separate gene pools seems evident.

Lindsey et al. presumed that the origin of two "species" in each pair occurred in allopatry, although they entertained the

possibility that the genesis was sympatric. Kirkpatrick and Selander (1979) also viewed the dwarf and normal populations in Maine lakes as "distinct independent gene pools, that is, species" though they commented that "All populations of lake whitefishes are closely similar genetically ...." Svärdson (1961, 1979), too, regarded speciation as complete in paired sympatric stocks. Kennedy (1943) and Fenderson (1964) treated the sympatric pairs of lake whitefishes as single species but believed the populations to be genetically distinct.

We interpret the paired, sympatric lacustrine morphs of lake whitefishes as genetically based stocks, and reject their interpretation as distinct species. Use of the term semispecies has been used to indicate incipient status, but adds little to understanding. "Stocks" surely have the potential, with time, of evolving into species. That coregonines are highly plastic and respond to the environment in growth rate, longevity, spawning habits, body proportions, and many meristic characteristics has been emphasized by Hile (1937) and Svärdson (1950, 1957, 1970). Most authors have relied heavily on gill-raker counts in the taxonomy of coregonines, and Svärdson (1970) viewed them as stable and reliable genetic markers of populations. Although we agree that gill-raker numbers are excellent characters, we note that they are strongly subject to selection and are also environmentally labile (Todd et al. 1981). When whitefish with extreme gill-raker counts were used as parents in an artificial-selection experiment, they yielded offspring of notably different mean values, 33.8 to 38 or 39 (Svärdson 1957), a result interpreted as due to polygenic inheritance. In a study of lake whitefish from seven interconnected lakes in Manitoba, presumably of recent common origin, Kliewer (1970) found highly significant variation in mean counts, which varied from 26.5 to 28.9. Substantial differences in mean counts were recorded by Lindsey et al. (1970, p. 131) in adjacent areas as well as in sympatric pairs throughout the North American range. Although the role of environmental effects on development cannot be ruled out, we suggest that the observed differences, whether of allopatric or sympatric occurrence, stem largely from natural selection. Sympatric genetic stocks with different gill-raker number presumably result from adaptation of different spawning aggregations to spatially or temporally different zooplankton sizes and concentrations. Later, selected differences in gill-raker numbers may be accentuated by character displacement. Although the differences in counts in lake whitefish stocks are modest, the same process extended through time could reasonably produce the greater differences found in stocks of ciscoes in the Great Lakes by Koelz and of whitefishes in Swedish lakes by Svärdson.

Coregonus artedii, unlike *clupeaformis*, is not represented by any closely related Beringian form. It persists in a few localities in the Mississippi drainage and presumably survived the last glaciation in that drainage. Morphological comparison indicates that the other forms of Great Lakes *Coregonus* (except *clupeaformis*) are more closely related to *artedii* than to any northwestern species. We reject the imaginative suggestion of Svärdson (1979) regarding the Pleistocene derivation of some of these stocks (e.g. *C. nipigon*) from Eurasia. There is no evidence to support this view. In contrast, *Prosopium cylindraceum*, with disjunct Arctic and Great Lakes populations (McPhail and Lindsey 1970), illustrates the kind of pattern that suggests Bering and southeastern refuges.

The apparent lack of lake-specific stocks of ciscoes outside the upper basins (except *kiyi orientalis* in Lake Ontario) could be taken as evidence that allopatric differentiation among lakes has been less significant than sympatric differentiation within the upper lakes. In particular, it is surprising that more distinct stocks are not present in Lakes Erie, Winnipeg, and Ontario. The shallowness and lack of habitat are cited as reasons for the low diversity (one or two stocks) in Lake Erie. Lake Winnipeg is even shallower.

The rich fauna of Lake Nipigon provides key zoogeographic evidence. Several of the stocks that inhabit this moderately large lake are similar to counterparts in Lake Superior. The falls near the head of the Nipigon River are a barrier to dispersal of lake fishes northward from Superior to Nipigon. We might suspect that such forms as *artedii*, *zenithicus*, *reighardi dymondi*, and *hoyi* dispersed southward into the Great Lakes from the northwest through Lake Kelvin (Nipigon basin). However, northward dispersal into the Nipigon basin was possible through the Black Sturgeon outlet between lakes Kelvin and Superior about 9000 yr ago (Zoltai 1965) and through the connection between the Superior and Nipigon basins through Lake Nakina at about the same time (Zoltai 1967b). Evidently these connections enabled dispersal of stocks from the Superior basin to the Nipigon basin about 9000 yr ago, early in the history of deglaciation of the basins. This interpretation suggests that much of the differentiation of these cisco stocks was already established relatively early, possibly before deglaciation. The alternative hypothesis requires rapid divergence 12 000–9000 yr ago. Our studies and those of Todd and Smith (1980, and unpublished data) indicate that most of the ciscoes and chubs in Lakes Nipigon and Superior form pairs of slightly differentiated complementary forms. We conclude that the differentiation of *artedii*, *hoyi*, and *zenithicus* occurred before or shortly after the lakes came into existence and before extensive isolation among basins. This implies that the differentiation occurred during the 70 000 yr of Wisconsinan time or before, although rapid evolution in early postglacial times is also a possibility. Todd has suggested (personal communication, 1980) that *C. nipigon* and *nigripinnis regalis* of Lake Nipigon are possibly stocks derived from Lake Agassiz, following differentiation in the Mississippi basin or in Lake Agassiz.

The possible antiquity of the stocks and their apparent stability, except recently, supports the hypothesis that ciscoes had achieved some extrinsic reproductive isolation, yet most of the evidence cited in the previous section does not suggest intrinsic reproductive isolation.

Implications of the Stock Concept

We define stocks as local populations that maintain recognizable genetic differentiation by separation of their spawning place or time. They are not intrinsically reproductively isolated from other stocks. (Subspecies, on the other hand, are usually allopatric or contiguous populations that are morphologically distinct at about the level of 95%. Species are morphologically distinct and for the most part reproductively isolated.) Koelz (1929, p. 333–334) recognized that differences between populations were probably maintained by tendencies to spawn in specific places at distinct times. This idea

has been further developed by a number of other workers, e.g. Smith (1964). Todd and Smith (1980) and Todd (1981b) show that in Lake Superior, populations that are separated geographically differ by comparable magnitudes to those separated by spawning times.

The existence of isolation by differences in spawning time or place does not require intrinsic isolating mechanisms. Supposed recent introgression might be evidence against the existence of intrinsic isolating mechanisms among the morphotypes of ciscoes and chubs. Most biologists who have worked with these fishes during the recent past have noticed that as populations declined to low densities, intermediate, difficult-to-identify individuals became more common in samples (Smith 1964). The implication is that as a population became rare the tendency to spawn with the wrong group increased.

The same biological characteristics that lead to mixed spawning by rare forms might be related to the observed tendencies of these fishes, when abundant, to segregate by different spawning time and place. Our hypothesis is that during the Pleistocene, as North American coregonine fishes were repeatedly displaced at the edges of advancing and retreating glaciers, a selective trade-off existed between the advantages of breeding at those places and times associated with past success (as indicated by homing aggregations of large numbers of spawners) and the alternative, i.e. breeding at times and places where competition was reduced. The inexorable creation and destruction of periglacial lakes made the latter behavior a rare, but occasionally significant, route to success. But in the majority of times and environments successful reproduction and recruitment occurred at, and was selectively controlled by, the time and place of successful reproduction in previous years. When population densities were high, as they were in the historic past and must have been generally in hundreds of slowly changing habitats during the Pleistocene, colonization of new spawning places and times was accomplished by stragglers. Yet as a general rule, most individuals must have returned to the grounds where their parents spawned, and at the time and temperature that was successful as demonstrated by the large numbers of breeding individuals responding to the same conditions. Central to this hypothesis is the possibility that the large numbers could constitute a stimulus leading an individual to a high probability of reproductive success.

We assume, on the basis of inference from aspects of life history and natural selection, that homing fishes that spawn communally not only are guided by stimuli related to time and place, but to large aggregations. If size of aggregation is a behavioral stimulus, under low density higher proportions of individuals will be attracted to large, spatially or temporally adjacent spawning aggregations, even if they involve other stocks. Thus, more hybrids will result. Hubbs (1955, p. 18) noted higher incidence of hybrids when one parental population is in low density.

The management significance of this hypothesis is that if intrinsic reproductive isolation does not exist, the possibility of hybridization of a rare form with a more common relative is a much more powerful cause of extinction. A rare, non-hybridizing species has a chance to persist for many generations. A stock vulnerable to hybridization, however, will disapper rapidly if a larger, related stock is available to absorb spawnings (and support exploitation). Some evidence for the vulnerability of cisco populations was seen early by Koelz (1929) and Van Oosten (1929, 1931). Smith and Van Oosten (1940) demonstrated aspects of the local nature of coregonines. The conclusion is that if sympatric populations are not intrinsicially reproductively isolated, the genetic diversity that permitted adaptation to different depths and habits will tend to be more vulnerable to elimination.

In conclusion, the evidence suggests that although reproductive isolation existed among partially differentiated stocks of ciscoes, such isolation was not stable, and the stocks have become extinct, with some terminal introgression. The stocks seem to represent no more than three or four (*artedii*, *hoyi*, *zenithicus*, *reighardi*), and possibly as few as one (*artedii*) species of cisco.

The Alien Component

Twenty-one (12%) of the total of 180 fish kinds in the Great Lakes basin are not native to the system (Tables 2, 3), and the number is growing. Of these, 14 were probably willfully or intentionally introduced, 5 took advantage of man-made canals, and 2 were unintentional introductions. The latter are the alewife (*Alosa pseudoharengus*), which colonized Lake Ontario in the early 1870s following accidental inclusion in stocking shad, later invading the upper lakes, and the Oriental weatherfish (*Misgurnus anguillicaudatus*), an escaped aquarium fish. In addition, four species originally native in the Lake Ontario basin have reached the upper lakes, the sea lamprey (*Petromyzon marinus*) and the American eel (*Anguilla rostrata*) by canal connections and the Atlantic salmon (*Salmo salar*) and margined madtom (*Noturus insignis*) by introductions.

The presence of the new forms raises questions as to their source, the reasons for their appearance in the basin, their success, their ecological role in the system, and their importance to human welfare. Among the 21 forms, 4 are introductions from Europe or Asia, 5 are from western North America, 6 are from eastern freshwaters or the Atlantic coast, of which 4 are introduced and 2 utilized canals, and 6 are native to the Mississippi basin, 3 each having entered the system by canals and by human transfer. Several, probably many, additional species have in the past been introduced into the Great Lakes basin but are not known to persist. Atlantic shad (*Alosa sapidissima*) were introduced into Lake Ontario in 1870 and survived until the 1920s when they apparently disappeared. Grass carp (*Ctenopharyngodon idella*) have been stocked repeatedly in the Great Lakes basin (V. Guillory in Lee et al. 1980, p. 151), but we have no evidence of reproduction here. A plethora of tropical and subtropical ornamental aquarium fish have surely been released into the Great Lakes drainage only to perish in the ensuing winter.

More than half of the exotic species are presently of minimal importance in the basin, being localized geographically, rare, or small and apparently unimportant ecologically. The several species of Pacific salmon, rainbow and brown trout, in contrast, are much valued as recreational fishes and some of these are abundant and widespread. Another group of species includes the widely distributed and abundant alewife, smelt, common carp, white perch, and the locally abundant goldfish. These are more or less controversial, being various-

ly valued as sources of food or recreation, but with negative ecological attributes (e.g. periodic alewife dieoffs, unfavorable competitive interactions with native species or environmental impacts, and predation). The sea lamprey, an exotic to the upper lakes, has played an overwhelming role in the history and fisheries of the basin.

Acknowledgments

The distributional data in our tables are the assembled accumulation over a long period by numerous persons, many cited in the bibliography or mentioned in those publications. We thank all of the many others who have contributed to our knowledge of Great Lakes fishes. We have benefited from discussions of coregonine systematics with Walter Koelz and thank him for his tolerance of our idiosyncracies. Ralph Hile, W. B. Scott, and S. H. Smith have all debated whitefish classification with us to our great advantage, but this does not imply their agreement with our interpretations. C. Lavett Smith and F. C. Rohde have provided information on distribution, and several participants in the STOCS symposium, especially W. J. Christie, J. J. Collins, D. P. Dodge, H. A. Regier, and T. N. Todd have furnished appreciated assistance. In review and discussion of this manuscript we are particularly indebted to E. J. Crossman and C. C. Lindsey, both of whom have advised freely and extensively. Dr Lindsey, however, disagrees with some of our speculations about *Coregonus*. We are indebted to the Geological Survey of Canada, Ottawa, for permission to publish Fig. 2–9 from Prest (1970). W. R. Farrand called our attention to geological references. We appreciate the assistance of Ruth Elder, Linda Krakker, Evelyn Peer, Donna Robins, and Beverly Smith in preparing the manuscript.

NOTE: Not all references listed are cited in the text. See Table 3 for explanation.

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Genetic Perspectives of the Identification and Conservation of Scandinavian Stocks of Fish[1]

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RYMAN, N., AND G. STÅHL. 1981. Genetic perspectives of the identification and conservation of Scandinavian stocks of fish. Can. J. Fish. Aquat. Sci. 38: 1562 – 1575.

Intraspecific planting and introduction of new species of fish has been much more restricted in northern Scandinavia than in many other parts of the world. Further, the general geography, with a large number of independent drainages and numerous impassable waterfalls, often prevented extensive spread of planted freshwater fish. Therefore, the genetic patterns observed among Scandinavian populations, e.g. their structure and the amount of distribution of genetic variation, may more accurately picture a natural situation than that reflected by stocks which have been influenced by a variety of fishery management activities. Natural populations of Scandinavian salmonids seem to be characterized by a more apparent subdivision than is usually observed, and multiple cases of genetically distinct sympatric demes have been identified within many species. Detailed electrophoretic analyses of natural populations have revealed the existence of previously unrecognized reproductive units exhibiting quite different ecological and morphological characteristics. At least in the brown trout (*Salmo trutta*), these units seem to have evolved independently, and there are no indications that they reflect the existence of two or more widespread sub- or sibling-species. In several cases attempts to preserve, in hatcheries, the genetic characteristics of endangered or unique remnant natural populations have proven unsuccessful; genetic changes and loss of genetic variability have occurred during the stocking. There is also strong evidence that planted hatchery fish have hybridized and drastically altered the genetic composition of valuable remnant natural populations. We discuss the ecological and fishery management implications of these findings and indicate some of the problems which we consider important to be addressed in future research.

Key words: genetic characteristics, Scandinavian salmonids, sympatric demes, identification, conservation

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L'ensemencement et l'introduction intraspécifiques de nouvelles espèces de poissons ont été beaucoup plus limités en Scandinavie septentrionale que dans plusieurs autres parties du monde. En outre, le grand nombre de bassins hydrographiques indépendants et de chutes infranchissables qui caractérisent la géographie générale ont souvent empêché une large dissémination de poissons d'eau douce introduits. Il se peut donc que les caractéristiques génétiques observées chez les populations scandinaves, p. ex. leur structure et l'ampleur de distribution de la variation génétique, reflètent plus fidèlement la situation naturelle que les stocks touchés par diverses activités de gestion de pêche. Les populations naturelles de salminidés scandinaves semblent être caractérisées par une subdivision plus apparente que celle ordinairement observée, et, parmi plusieurs espèces, de nombreux cas de dèmes sympatriques génétiquement distincts ont été reconnus. Des analyses électrophorétiques détaillées de populations naturelles ont permis de détecter des unités reproductrices jadis méconnues, montrant des caractéristiques écologiques et morphologiques fort différentes. Ces unités, au moins chez la truite brune (*Salmo trutta*), semblent avoir évolué indépendamment et on n'a pas d'indications qu'elles reflètent l'existence de deux ou plusieurs sous-espèces ou espèces jumelles largement répandues. Les efforts en vue de maintenir, chez les poissons d'élevage, les caractéristiques génétiques ou de préserver les restes de populations naturelles menacées

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ou uniques ont échoué dans bien des cas; des changements génétiques et une perte de variabilité génétique se sont produits au cours de l'ensemencement. Il y a aussi de bonnes indications que les poissons d'élevage introduits se sont croisés avec les restes précieux de populations naturelles et en ont modifié dramatiquement la composition génétique. Nous analysons les implications écologiques et de gestion des pêches de ces observations et mentionnons quelques-uns des problèmes jugés suffisamment importants pour être l'objet de recherches futures.

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THE stock concept, i.e. the observation that a species is subdivided into more or less genetically different subunits, has been recognized intuitively for many Scandinavian fish species, in particular the salmonids. The basis for this recognition is the existence of striking ecological and phenotypic differences between fish from different lakes, spawning sites, or spawning seasons. A hereditary background for this phenotypic variation was first proven by the now classical works by Alm (1946, 1949, 1959). Subsequent studies by other investigators further substantiated the genic basis for at least part of the variation of intraspecific ecological and morphological characters (e.g. Carlin 1965; Nyman 1972; Henricson and Nyman 1976; Ryman 1970, 1972a, b; Svärdson 1970, 1979, and references therein).

A considerable portion of the variability of morphological characters is determined by nongenetic factors (e.g. Falconer 1960). Therefore, assessment of evolutionary relationships or estimation of the amount and distribution of genetic variation cannot be based exclusively on analyses of phenotypic characteristics, e.g. body size and shape, coloration, or number of vertebrae. Morphological studies have helped in explaining the diversity within species (e.g. Svärdson 1979), but many studies of phenotypic variation have been statistically inadequate. This lack of reliable data has often prevented identification of subunits, or has overemphasized the genetic control of morphological characters that are also influenced by the environment.

A major reason for this lack of data is most likely because most Scandinavian hatcheries are constructed with the primary aim of raising a large number of fish; they do not permit controlled breeding or experiments on the rearing of progeny groups in different environments. It is only recently that detailed experiments for the estimation of environmental and genetic variance components for economically important characters have been made (Gjedrem 1976; Gunnes and Gjedrem 1978; Naevdal et al. 1978; Refstie and Steine 1978; Refstie et al. 1977; Aulstad et al. 1972, and references therein).

Accurate estimates of the relative importance of environmental and genetic factors for the variation of characters such as growth rate, survival, and disease susceptibility are basic prerequisites for the construction of successful breeding programs. It must be emphasized, however, that such estimates only refer to particular experimental conditions and that they constitute relative, and not absolute, measures of the amount of genetic variation. The classical techniques of animal breeding refer to "statistical" genes rather than to distinct alleles at particular loci. Therefore, they are generally of little use for stock identification, quantitative estimates of genetic identity, or assessment of evolutionary relationships. It was not until electrophoretic techniques became available that a more detailed examination of intraspecific genetic relationships became possible. The first electrophoretic analyses that dealt with variation at single loci confirmed the existence of genetically differentiated subunits in several species, e.g. Atlantic cod (*Gadus morhua*) (Sick 1961; Frydenberg et al. 1965), herring (*Clupea harengus*) (Naevdal 1969, 1970), Atlantic salmon (*Salmo salar*) (Payne et al. 1971; Nyman and Pippy 1972; Child et al. 1976), and Arctic char (*Salvelinus alpinus*) (Nyman 1972).

A large number of genetic loci must be examined for detailed genetic analysis of populations structure (Lewontin 1974; Nei and Roychoudhury 1974; Nei 1975; Allendorf and Utter 1979). It is only recently that more detailed genetic studies based on a large number of loci have been performed for quantitative estimation of the amount and pattern of genetic diversity in Scandinavian fish species such as herring (Anderson et al. 1981), cod (Mork et al. in press), Atlantic salmon (Khanna et al. 1975a, b; Ståhl 1981; this paper), Arctic char (this paper), perch (*Perca fluviatilis*) (Gyllensten et al. personal communication), brown trout (*Salmo trutta*) (Allendorf et al. 1977; Ryman et al. 1979; this paper), and whitefish (*Coregonus* spp.) (Ferguson et al. 1978; Vuorinen and Lankinen 1978; Vuorinen et al. 1981).

From a general perspective, Scandinavia constitutes a unique area for the study of the genetic structure among natural fish populations. Although transfer of fish from one lake to another has been practiced locally for a long time (Svärdson 1979), intraspecific plantings and introduction of new species of fish have been much more restricted in northern Scandinavia than in many other parts of the world. Further, the general geography, with a large number of independent drainages and numerous impassable waterfalls, often prevented the extensive spread of planted freshwater fish. Therefore, the genetic patterns observed among Scandinavian fish populations may more accurately reflect a natural situation, with regard to the structure and the amount and distribution of genetic variation, than populations that have been much more strongly influenced by human activities. It is the purpose of this paper to present electrophoretic data indicating a much more complicated population structure than was previously recognized among natural populations of three species: Arctic char, Atlantic salmon, and brown trout. The variability patterns will be compared with that observed among populations that have been influenced by various human activities. We present evidence that currently practiced management procedures have generated genetic changes in both natural and hatchery populations. Some of these issues have been discussed previously; the current presentation reviews complements, and extends those results.

Materials and Methods

The data have been collected for various purposes within the scope of our ongoing study of genetic variability and population structure in different fish species. The geographic location of collection sites is given in Fig. 1. Routines for collection and storage of tissue samples have been described previously, as have the electrophoretic techniques and staining procedures (Utter et al. 1974; Allendorf et al. 1977; Ryman et al. 1979; Ståhl 1981).

In addition to use of amido black general protein stain, all or most of the following enzymes (abbreviations in parenthesis) were stained for in all three species: aspartate aminotransferase (AAT), alcohol dehydrogenase (ADH), α-glycerophosphate dehydrogenase (AGP), adenylate kinase (AK), aldolase (ALD), creatine phosphokinase (CPK), diaphorase (DIA), esterase (EST), fructose-1,6-diphosphatase (FDP), fumarase (FUM), glyceraldehyde-3-phosphate dehydrogenase (GAPDH), glutamate dehydrogenase (GDH), glucose-6-phosphate dehydrogenase (G6PDH), β-glucoronidase (GUS), hexokinase (HK), isocitrate dehydrogenase (IDH), leucine aminopeptidase (LAP), lactate dehydrogenase (LDH,

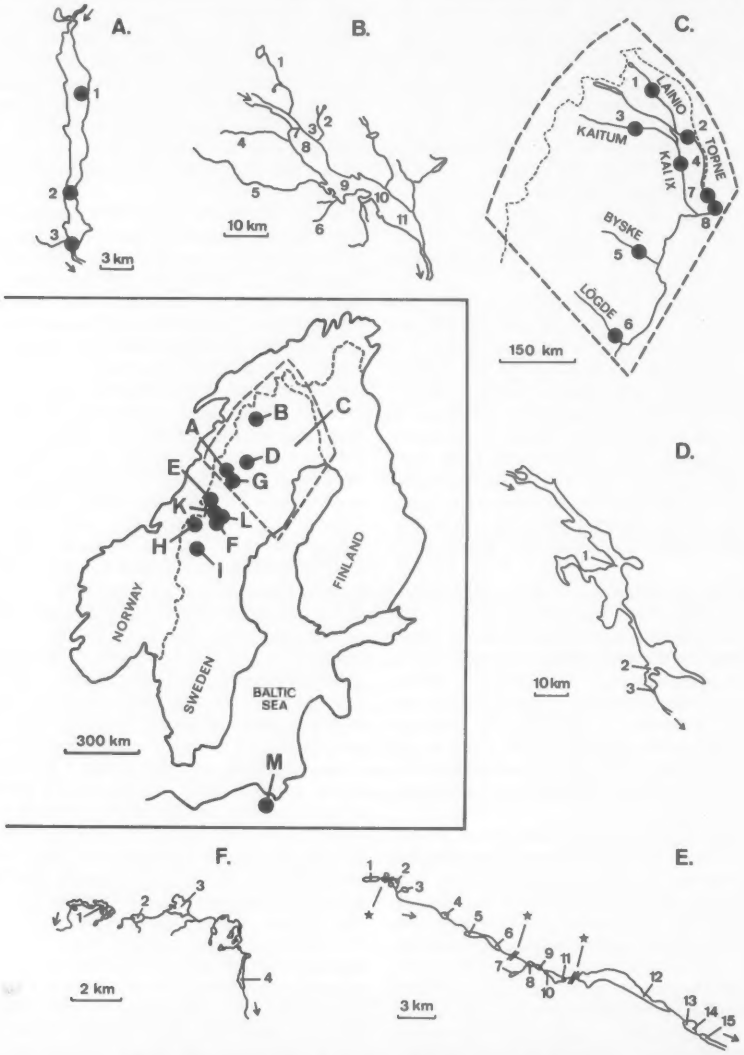

FIG. 1. Geographic location and detailed maps of collection sites.

malate dehydrogenase (MDH), malic enzyme (ME), peptidase (PEP), 6-phosphogluconate dehydrogenase (6PGDH), phosphoglucose isomerase (PGI), phosphoglucomutase (PGM), phosphomannose isomerase (PMI), sorbitol dehydrogenase (SDH), superoxide dismutase (SOD), and xanthine dehydrogenase (XDH).

The system of nomenclature for designation of electrophoretically detected loci and alleles follows Allendorf and Utter (1979). An abbreviation is chosen to designate each protein; when in italics, these same abbreviations represent the loci coding for these proteins. In the case of multiple forms of the same enzyme, a hyphenated numeral is included: the form with the least anodal migration is designated one, the next two, and so on. Allelic variants are designated according to the relative electrophoretic mobility. One allele (generally the most common one) is arbitrarily designated *100*. This unit distance represents the migration distance of the isozyme coded for by this allele. Other alleles are then assigned a numerical value representing their mobility relative to this unit distance. Thus, an allele of the least anodal LDH locus, coding for an enzyme migrating one-half as fast as the common allele product, would be designated *LDH-1(50)*.

The genetic interpretation of electrophoretic banding patterns in brown trout has been previously described by Engel et al. (1971), Allendorf et al. (1977), May et al. (1979), Utter et al. (1979), and Taggart et al. (1981), and those in Atlantic salmon by Ståhl (1981), Cross et al. (1979) and Cross and Ward (1980). In addition to previously reported polymorphisms in brown trout, the segregation of a fast (*110*) allele at *PGI-3* was observed in the present study; a similar segregation pattern at the same locus has also been observed in some Irish brown trout populations (A. Ferguson personal communication). For technical reasons, different numbers of loci are surveyed in different samples; up to 54 and 45 loci were scored in brown trout and Atlantic salmon, respectively.

Interpretation of the banding patterns observed for Arctic char followed the same principles as have been previously outlined with special reference to brown trout population data (Allendorf et al. 1977). A detailed report on locus expression and tissue predominance will be published separately. A total of 37 loci usable for population screenings were identified, and three of these (*EST-2*, *LDH-3*, and *MDH-4*) were variable in one or more samples, each locus segregating for two alleles. The *EST-2* polymorphism (alleles *100* and *90*) was proven to be identical with the serum esterase polymorphism previously described by Nyman (1972); in the course of the present study, that locus was scored in eye or muscle tissue (we are indebted to Mr R. Gydemo for tissue samples from a large number of specimens that had been independently scored for serum esterase variability which made this comparison possible). A fast allele (*130*) was observed at one of the duplicated loci (*MDH-3* and *4*) coding for the muscle form of MDH. These loci share alleles with identical electrophoretic mobility and are most commonly represented by a single band on the gel. Although it is impossible to assign that allele to a specific locus (i.e. *MDH-3* or *4*), it was arbitrarily assigned to *MDH-4*. In addition to the common (*100*) allele at *LDH-3*, a single copy of a variant (*75*) allele was observed at this locus. No variation was observed at the remaining loci scored: *AAT-2*, *ADH*, *AGP*, *AK-3*, *CK-1,2,3*, *EST-1,3*, *GAPDH-1,2*, *GUS*, *IDH-1,2*, *LDH-1,2,4,5*, *MDH-1,2,3*, *ME-1,2*, *6PGDH*, *PGI-1,2,3*, *PGM-1,2*, *PMI*, *SDH*, *SOD*, *XDH*, and an unidentified muscle protein represented by a single invariant band.

For the following species/locus combinations, allele frequencies were estimated from the square root of the frequency of the only genetically defined genotype. Brown trout: *CPK-1* (occasionally, allele counting was possible in fresh samples), *MDH-4*, and *LDH-5*; Atlantic salmon: *SDH-1*. Other allele frequencies were determined by direct allele counting. Statistical tests for gene frequency heterogeneities were correspondingly based on allele and phenotype counts, respectively (cf. Allendorf et al. 1977). The occurrence of skewed allele frequencies combined with limited sample sizes occasionally resulted in too small expectancies for proper χ^2 evaluations; in those cases exact tests were also applied (Sokal and Rohlf 1969, chapter 16) to validate the conclusions drawn from the χ^2 test statistics and to minimize the frequency of type I statistical errors.

Population Structure

The general pattern for the distribution of genetic variation indicates a complex population structure and considerable genetic heterogeneity over very small geographical areas within all the three species studied. The data available also indicate that these genetic differences are coupled with ecological and morphological divergence.

Brown Trout

The best example of population subdivision on a microgeographic scale is the brown trout of Lake Bunnersjöarna (Ryman et al. 1979). Lake Bunnersjöarna is an oligotrophic mountain lake (*1*; Fig. 1) at an elevation of 955 m, located in the uppermost part of the River Indalsälven drainage system flowing into the Baltic Sea. The lake is usually frozen over from October to the beginning of June. Brown trout are the only fish occurring in the lake; Arctic char was introduced in the 1950s, but is no longer present. As indicated by the Swedish name (plural), Lake Bunnersjöarna is actually a pair of twin lakes. They are connected through a 50-m channel with a depth of about 1 m, permitting bidirectional migration between the lakes. Such migration has been observed many times and appears to occur frequently. Each lake has an area of about 40 ha. The southern lake is shallow (0.5–1.5 m); the northern lake is somewhat deeper (1–5 m) and is largely without shallow banks.

Two sympatric populations of brown trout with apparently complete reproductive isolation exist in these lakes. This was detected during the routine electrophoretic analysis of fish from several randomly sampled lakes. The existence of these two reproductively isolated subpopulations (demes) was initially indicated by an apparent absence of heterozygotes at a lactate dehydrogenase locus (*LDH-1*) segregating for the two alleles *100* and *240*; only the two homozygotes were observed, and these occurred at approximately equal frequencies. Subsequent analysis of the variation at seven additional polymorphic loci confirmed the conclusion that two reproductively isolated demes occur sympatrically in Lake Bunnersjöarna.

One of the most important observations about the two demes is the extremely small amount of genetic divergence

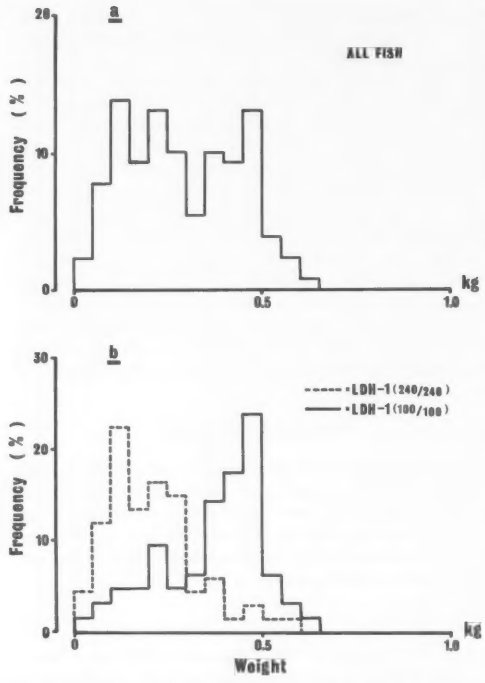

FIG. 2. Distribution of weights (kg) in a sample of 5-yr-old brown trout from Lake Bunnersjöarna, central Sweden. (a) The total material; number of fish = 130. (b) Separate distributions for the two populations classified according to the *LDH-1* genotypes. (---) *LDH-1(240/240)*; number of fish = 67. (—) *LDH-1(100/100)*; number of fish = 63.

between them. The genetic distance (Nei 1975) is only 0.025 as estimated from 54 electrophoretic loci. Genetic distances of this magnitude are typical for local populations of the same species. To our knowledge, these two demes of brown trout represent the least genetically divergent, reproductively isolated sympatric pair of vertebrate populations that have yet been identified.

It is important to realize that the small amount of electrophoretically detectable genetic divergence between the demes does not imply that such genetic differences can be ignored, or that they largely reflect ecological and evolutionary "noise." On the contrary, the ecological and morphological characteristics of the two demes appear to be quite different. Growth patterns are different, as illustrated by the distributions of weight among 5-yr-old fish (Fig. 2). A considerable portion of the variation of weights in the mixed sample was actually due to differences between demes. Without the proper information concerning the population structure, the size variation in the mixed sample (Fig. 2a) would have been misinterpreted as "natural" and statistically unexplained body size variation within an age-class. The distribution of the demes between lakes reflects behavioral differences also. Fish from those demes occur frequently in both lakes, but differ in their relative occurrence in each lake. Finally, detailed examination of a number of morphometric characters revealed small but clear-cut differences, which most likely reflect different ecological specializations with regard to feeding behavior and food preferences (Behnke et al. unpublished data).

There is no evidence that the two demes in Lake Bunnersjöarna reflect the occurrence of two widespread sub- or sibling-species characterized by contrasting homozygosity at the *LDH-1* locus. We have analyzed large numbers of brown trout populations over much of Scandinavia, but never observed fixation for the *LDH-1(240)* allele in another population. Most brown trout populations are monomorphic for the *LDH-1(100)* allele, but several populations (unpublished data) have been observed that are segregating in Hardy–Weinberg proportions for both alleles. It seems to be a general tendency for brown trout to aggregate into close and genetically distinct subpopulations, and in Lake Bunnersjöarna the two demes happened to become fixed for different alleles which facilitated a more detailed examination of these populations.

The apparent generality of genetic heterogeneity within restricted geographic areas is supported by electrophoretic data from natural brown trout populations in Northern Ireland (Ferguson 1980; Ferguson and Mason 1981); we provide examples from additional lake/river systems from different parts of Sweden, i.e. Lake Tärnasjön (*A 1–3*), Lake Lulejaure with tributaries (*B 1–11*), and River Storån (*E 1–15*) (Fig. 1 and Table 1).

Samples from the River Storån (*E 1–15*) provide an excellent example of pronounced genetic diversity over small geographic distances. There are three waterfalls (★) in the area. No tagging experiments have been performed so we cannot positively prove that these falls prevent upstream migration of brown trout. However, the falls have been efficient in stopping upstream migration of other fish species. Brown trout are the only species occurring at *E 6* and upstream; Arctic char are found in *E 7* and downstream, and in Lake Stora Jougdan (*E 12*) and downstream there are also perch (*Perca fluviatilis*) and whitefish (*Coregonus* spp). It appears that brown trout can migrate downstream through the whole river system; however, the falls most likely prevent upstream migration.

These apparent migration hindrances seem to explain part of the differentiation within this river system. On the average, when moving downstream there is a decreasing frequency of the *AGP-2(100)* allele, and an increasing frequency of the *CPK-1(100)* allele. *MDH-2* appears to be fixed for the *100* allele in *E 1–2*, while this locus segregates with a generally decreasing frequency of the *100* allele in the lakes located downstream, and a similar pattern is observed at *PGI-3*.

The levels of genetic variability, as measured by the frequency of polymorphic loci (*P*) and average heterozygosity (*H*), tend to be higher in the lower part of the system than in the upper part. Such a continuously increasing level of genetic variation is expected if gene flow is unidirectional, so that genetic variation in the populations in the upper (end) part of the system cannot be increased by migration from genetically different populations.

Although part of the allele frequency differences observed between the locations *E 1–15* may be explained by geographical barriers, a closer inspection of Table 1 reveals still more striking differences between closely located collection

sites in the absence of apparent hindrances for bidirectional migration. Chi-square contingency tests confirm the existence of significant allele frequency differences among the *E 7–11* locations at both polymorphic loci samples ($\chi^2_4 = 9.82$, $P < 0.05$ and $\chi^2_4 = 77.52$, $P < 0.001$ at *AGP-2* and *CPK-1*, respectively). A similar pattern of differentiation is also found among the *E 12–15* sampling sites where allele frequencies differ significantly at the *MDH-2* locus ($\chi^2_3 = 8.89$, $P < 0.05$) and the sum of chi-squares over all polymorphic loci is also close to significance ($\chi^2_{12} = 20.73$, $P \approx 0.05$). The most conspicuous deviation from a clinal pattern is found in the upper part of the river system, where the allele frequency at *CPK-1* in lake *E 2* deviates dramatically from that of the neighboring lakes ($\chi^2_3 = 72.83$, $P < 0.001$ when comparing *E 1–6*, and $\chi^2_2 = 38.24$, $P < 0.001$ when testing for homogeneity among *E 2–4*).

A detailed examination of growth patterns and other morphological characteristics has not been completed yet, but particularly in the upper part of the system (*E 1–4*) the fishing is "good", resulting in a considerable portion of fish larger than 1 kg. The *E 2* collection site represents the only exception and no fish larger than 0.2 kg was caught in that lake. The fishing rights in this area belong to the Lapps, and it is an interesting observation (reflecting a general phenomenon) that the only lake in the system inhabited by a population with poor production characteristics has not been named by the Lapps. In contrast, Lake Boultenjaure (*E 3*) gave by far the best result as measured by fish size and fishing effort, although it is too small to "deserve" a Lappish name. Although speculative, this indicates that the morphological differences may have prevailed for a long period of time, and we consider it an important observation that these body size extremes coincide with the allele frequency extremes at the only locus found to be polymorphic in this part of the river system.

There is also some evidence of the existence of more than one population in Lake Stora Petter–Lars (*E 10* and *11*), as indicated by allele frequency differences at *AGP-2* and *CPK-1* between the inlet (*E 10*) and outlet (*E 11*) samples. Admittedly, the statistical basis for such a conclusion is weak. The skewed allele frequencies complicate the statistical analysis and the difference is insignificant at both loci ($0.10 > P > 0.05$ in both cases). However, adding the two chi squares for a joint evaluation (Yate's correction not applied; cf. Sokal and Rohlf 1969, p. 590) yields $\chi^2_2 = 5.99$ ($P < 0.05$), supporting the concept of further subdivision within this small lake.

The apparent generality of population subdivision within single lakes is further substantiated by the allele frequency heterogeneities observed among the three sampling sites in Lake Tärnasjön (*A 1–3*). There are highly significant differences at both *AGP-2* and *PGI-3* (Table 1). The sum of the chi squares from all polymorphic loci ($\chi^2_8 = 68.97$, $P < 0.001$) indicates that these differences by no means reflect type I statistical errors.

This generality is further supported by the data from Lake Lulejaure (*B*), which represents a quite different habitat as compared to the lakes previously described. It is a large lake (Fig. 1B) with many tributaries. In addition to brown trout, it contains several other fish species, including Arctic char, burbot (*Lota lota*), northern pike (*Esox lucius*), perch (*Perca fluviatilis*), whitefish (*Coregonus* spp), and roach (*Rutilus rutilus*). We have samples from five collection sites in the lake (*site B7–11*) as well as from the tributaries (*site B 1–6*). The *B 2* and *3* collection sites represent two sampling localities in the upper and lower parts of the same (Såkasjokk) tributary, respectively (cf. Ståhl and Ryman 1979; Ryman 1981). The allele frequency distributions indicate a marked genetic heterogeneity among sampling sites in this area also (Table 1). There are highly significant allele frequency differences between tributaries at three of the four polymorphic loci, suggesting the existence of genetically distinct spawning populations in the different streams. The difference in allele frequencies at *AGP-2* between the upper and lower parts of the Såkasjokk stream (*B 2* and *3*) is also statistically significant ($\chi^2_1 = 7.46$, $P < 0.01$), indicating the existence of more than one spawning population within this stream.

With regard to the lake samples (*B 7–9*), the allele frequency distribution at *AGP-2* indicates considerable genetic heterogeneity among different locations within the lake. Summing the chi squares from all three polymorphic loci (*AGP-2*, *LDH-5*, *MDH-2*) further supports this concept ($\chi^2_{12} = 30.60$, $P < 0.01$). These genetic differences are coupled with growth pattern differences. An age-by-length growth curve of the von Bertalanffy type (Allen 1966) was fitted to the pooled material from the lake. The individual deviations from this average growth curve were analyzed by variance analysis and revealed significant age-corrected mean length differences among the five collection sites ($F_{4,67} = 5.81$, $P < 0.001$). We interpret these differences as evidence of behavioral and ecological differences between the spawning populations contributing to the brown trout community of Lake Lulejaure. This conclusion is further supported by a significant deficiency of heterozygotes at *AGP-2* ($\chi^2_1 = 4.48$, $P < 0.05$), as compared to the expected Hardy–Weinberg distribution; such heterozygote deficiency is expected in a mixed sample comprising fish from genetically distinct populations.

Productivity estimates and smolt counts have indicated that the Kaltisjokk stream (*site B 5*) contributes the major part of brown trout caught in Lake Lulejaure (Andreasson and Karlström unpublished data). It is an interesting observation that *CPK-1* is polymorphic in the sample from the Kaltisjokk stream, while no variability was observed in the lake samples. Although the difference is not significant ($P = 0.07$ using Fisher's exact test), these two pieces of information appear contradictory and compel some consideration when planning the management of this area.

It has been suggested that fish from the Kaltisjokk stream would constitute the most appropriate source for a brood stock producing fry for planting in Lake Lulejaure. The present data indicate that a more detailed examination of fish from the Kaltisjokk stream is needed to identify the number of populations potentially spawning in this stream. There is no reason to believe that Kaltisjokk should not be one of the major contributors of brown trout to Lake Lulejaure. It is possible, however, that several populations spawn there and that these populations are genetically different. When founding a brood stock for planting in Lake Lulejaure, the population that is adapted to that environment should be chosen to accomplish the goals of the stocking program (cf. Krueger et al. 1981).

Atlantic Salmon

A pattern of population subdivisions similar to that

TABLE 1. Allele frequencies and estimates of average heterozygosity (H) and proportion of polymorphic loci (P; 99% criterion) in samples from natural populations and hatchery stocks of brown trout. Bars (—) indicate that the locus was not scored in that sample. The H and P values are based on 34 (River Weichsel stock), 35 (map code *A* and *E* locations), and 54 (map code *I* locations) loci, respectively. (The total number of loci analyzed in other samples was too low to permit accurate estimation of H and P.) The River Weichsel stock is anadromous and the rest of the samples are from lacustrine populations (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).

Collection site/stock	Map code	Year of sampling	No. of fish	*AGP-2* (*100*)	*CPK-1* (*100*)	*EST-2* (*100*)	*LDH-1* (*100*)	*LDH-5* (*100*)	*MDH-2* (*100*)	*MDH-4* (*100*)	*PGI-3* (*100*)	*SDH-1* (*100*)	*SOD* (*100*)	*H* (%)	*P* (%)
Lake Jeriken	E 1	1977	99	1	0.304	1	1	1	1	1	1	—	1	1.2	2.9
Lake	E 2	1977	31	1	0.084	1	1	1	1	1	1	—	1	0.4	2.9
Lake Boultenjaure	E 3	1977	25	1	0.654	1	1	1	0.940	1	1	—	1	1.6	5.7
Lake Bursvattnet	E 4	1977	58	1	0.492	1	1	1	0.983	1	1	—	1	1.5	5.7
Lake Övre Hemsjön	E 5	1975	185	0.997	0.524	—	1	—	—	1	—	—	1		
Lake Nedre Hemsjön	E 6	1974	85	1	0.580	—	1	—	—	1	—	—	1		
Lake Butjärn	E 7	1976	112	0.951	0.457	—	1	—	—	1	—	—	1		
Lake Övre Petter–Lars	E 8	1975	78	0.936	0.747	—	1	—	—	1	—	—	1		
Lake Mellersta Petter–Lars	E 9	1976	110	0.905	0.684	—	1	—	—	1	—	—	1		
Lake St. Petter–Lars, inlet	E 10	1975–76	250	0.940	0.821	—	1	—	—	1	—	—	1		
Lake St. Petter–Lars, outlet	E 11	1976	88	0.977	1	—	1	—	—	1	—	—	1		
Lake Stora Jougdan	E 12	1977	39	0.936	0.774	1	1	1	0.885	1	0.949	—	1	2.2	11.4
Lake Stora Kalvan	E 13	1977	53	0.972	0.693	1	1	1	0.934	1	0.925	—	1	2.1	11.4
Lake Stora Kalvan, outlet	E 14	1977	22	0.955	0.631	1	1	1	0.773	1	0.886	—	1	3.2	11.4
Lake Övre Långvattnet	E 15	1977	16	0.875	0.567	1	1	1	0.812	1	1	—	1	2.9	8.6
			χ^2	86.78	250.07				59.68		38.73				
			df	14	14				7		7				
			P	***	***				***		***				
Tributaries to Lake Lulejaure															
Ruoktojokk	B 1	1977	65	0.962	0.785	1	1	0.691	0.938	1	1	—	1		
Såkasjokk (upper)	B 2	1977	26	0.827	1	1	1	0.877	0.865	1	1	—	1		
Såkasjokk (lower)	B 3	1977	25	1	1	1	1	0.800	0.980	1	1	—	1		
Tjegnaljokk	B 4	1977	25	0.860	1	1	1	0.529	0.980	1	1	—	1		
Kaltisjokk	B 5	1976	100	0.715	0.776	1	1	—	—	1	—	—	1		
Appakisjokk	B 6	1977	43	0.988	1	1	1	0.835	1	1	1	—	1		
			χ^2	66.80	6.02			18.44	15.64						
			df	5	5			4	4						
			P	***	n.s.			**	**						
Lake Lulejaure	B 7	1977	19	0.868	1	1	1	0.624	0.917	1	1	—	1		
Lake Lulejaure	B 8	1977	7	0.929	1	1	1	0.756	0.857	1	1	—	1		
Lake Lulejaure	B 9	1977	22	0.659	1	1	1	0.574	1	1	1	—	1		
Lake Lulejaure	B 10	1977	14	0.679	1	1	1	0.277	0.964	1	1	—	1		
Lake Lulejaure	B 11	1977	12	0.458	1	1	1	0.500	1	1	1	—	1		
			χ^2	15.93				6.57	8.10						
			df	4				4	4						
			P	**				n.s.	n.s						

TABLE 1. *(Concluded)*

Collection site/stock	Map code	Year of sampling	No. of fish	*AGP-2* (*100*)	*CPK-1* (*100*)	*EST-2* (*100*)	*LDH-1* (*100*)	*LDH-5* (*100*)	*MDH-2* (*100*)	*MDH-4* (*100*)	*PGI-3* (*100*)	*SDH-1* (*100*)	*SOD* (*100*)	*H* (%)	*P* (%)
River Skellefteälven															
Arjeplogströmmarna	D 1	1978	49	0.802	1	1	1	0.958	0.867	1	1	—	1		
Bergnäsälven	D 2	1978	51	0.853	0.860	1	1	0.939	0.922	1	0.951	—	1		
Slagnäsforsen	D 3	1978	50	0.790	0.859	1	1	0.990	0.830	1	0.990	—	1		
			χ^2	1.61	0.98			3.62	3.88		6.89				
			df	2	2			2	2		2				
			P	n.s.	n.s.			n.s.	n.s.		*				
Lake Tärnasjön	A 1	1977	91	0.918	0.531	1	1	1	0.555	1	0.890	—	1	3.8	11.4
Lake Tärnasjön	A 2	1977	76	0.954	0.513	1	1	1	0.559	1	0.974	—	1	3.2	11.4
Lake Tärnasjön	A 3	1977	28	0.679	0.500	1	1	1	0.536	1	0.696	—	1	5.3	11.4
			χ^2	35.22	0.14				0.09		33.52				
			df	2	2				2		2				
			P	***	n.s.				n.s.		***				
Lake Bunnersjöarna															
Deme I	I	1975–76	46–125	0.976	0.562	0.967	1	0.872	1	0.571	1	0.891	0.989	2.8	13.0
Deme II	I	1975–76	56–140	1	0.293	0.886	0	1	1	1	1	1	1	1.1	3.7
			χ^2	4.82	26.04	3.37		12.63		51.08		10.58	0.01		
			df	1	1	1		1		1		1	1		
			P	*	***	n.s.		***		***		***	n.s.		
River Weichsel hatchery stock derivatives	M														
Polish hatchery hatched	1977	1979	20	0.725	0.675	1	1	1	0.825	1	0.900	—	1	3.8	11.8
Kälarne hatchery, Sweden	1977	1979	50	0.610	0.850	1	0.770	1	1	1	1	—	1	3.2	8.8
Kälarne hatchery, Sweden	1977	1979	76	0.493	0.974	—	0.789	1	1	1	1	—	1		
Älvkarleby hatchery Sweden	1977	1979	48	0.563	1	1	0.885	0.791	0.875	1	1	—	1	3.7	11.8
Älvkarleby hatchery Sweden	1978	1979	83	0.470	0.994	—	0.759	1	1	1	1	—	1		
			χ^2	12.26	82.48		15.18	91.84	63.18		52.10				
			df	4	4		4	4	4		4				
			P	*	***		**	***	***		***				

observed in brown trout is also found among natural populations of Atlantic salmon. We have samples from Atlantic salmon parr collected during the fall of 1979 from six locations in four drainage systems in northern Sweden (Fig. 1C). None of these rivers has yet been affected by major man-made constructions and they still support naturally reproducing Atlantic salmon populations. The smolts from each locality were collected from a restricted geographical area (1000–7000 m^2 of the river) by electroshocking. Hatchery-reared Atlantic salmon have not been released into any of the sample areas *C 1–6*; therefore, each of those samples should represent the result of natural reproduction (Ståhl 1981).

There were highly significant allele frequency differences among samples collected in the field (*C 1–6*) at all polymorphic loci (Table 2) indicating considerable overall genetic heterogeneity among populations. There was also a statistically significant allele frequency difference at *AAT-3* ($\chi^2_1 = 8.35$, $P < 0.01$) between the Lainio (*C 1*) and Torne (*C 2*) rivers which both belong to the same main drainage system; this indicates the existence of genetic heterogeneity between, as well as within, major drainages.

Arctic Char

Previous electrophoretic studies on Arctic char revealed considerable genetic heterogeneity and a complex population structure in this species in Scandinavia (Nyman 1972; Henricson and Nyman 1976), as well as in the British Isles (Child 1977). The Scandinavian studies were all based on the segregation at an esterase locus (*EST-2* in the present nomenclature), and Child (1977) reports polymorphism at a transferrin locus, in addition to an esterase locus that appears to be identical with that examined by Nyman (1972), Henricson and Nyman (1976), and in the present study. Serum samples were not available for our samples, so we have not been able to test for transferrin polymorphism. Nevertheless, our results indicate low levels of electrophoretically detectable genetic variation in this species (Table 3). The variability pattern at the additional locus found polymorphic (*MDH-4*) confirms the results of previous studies and further supports the concept of considerable genetic heterogeneity within restricted geographical areas in this species also (Fig. 1, Table 3).

On the basis of the allele frequency distribution at the

Table 2. Allele frequencies in samples from six naturally reproducing Atlantic salmon populations and two hatchery stocks derived from the River Torne–Lainio drainage. The estimates of average heterozygosity (*H*) and frequency of polymorphic loci (*P*) are based on a total of 45 loci and are given for the samples where all those loci were surveyed. The field (river) samples were collected in 1979 (***$P < 0.001$).

Collection site/stock	Map code	No. of fish	*AAT-3* (*100*)	*ME-2* (*100*)	*PGM-1* (*100*)	*SDH-1* (*100*)	*H* (%)	*P* (%)
River Lainio	C 1	14	0.429	0.929	1	0.756	2.2	6.7
River Torne	C 2	100	0.720	0.950	1	0.781	1.9	6.7
River Kaitum	C 3	98	0.622	0.929	1	0.553	2.4	6.7
River Kalix	C 4	98	0.622	0.918	0.980	0.606	2.5	8.9
River Byske	C 5	59	0.890	0.720	0.856	0.677	2.9	8.9
River Lögde	C 6	69	0.986	0.819	1	0.552	1.8	6.7
		χ^2_5	97.40***	52.32***	86.65***	26.63***		
Torne–Lainio drainage hatchery stocks								
Kukkola	C 7	50	0.640	0.980	0.960	0.548	—	—
Torne river mouth	C 8	130	0.718	0.950	1	0.551	—	—

Table 3. Allele frequencies in samples from natural populations of Arctic char. The estimates of average heterozygosity (*H*) and proportion of polymorphic loci (*P*; 99% criterion) are based on a total of 37 loci (***$P < 0.001$).

Collection site	Map code	Year of sampling	No. of fish	*EST-2* (*100*)	*LDH-3* (*100*)	*MDH-4* (*100*)	*H* (%)	*P* (%)
Lake Gardiken	G	1979	82	0.683	1	0.750	2.2	5.4
Lake Munsvattnet	K	1978	58	1	1	1	0	0
Lake Lilla Stensjön	L	1978	45	1	1	1	0	0
Lake Trollsvattnen	F 1	1979	5	0.300	1	0.900	1.6	5.4
Lake Lilla Bävervattnet	F 2	1979	101	1	1	1	0.0	0
Lake Stora Bävervattnet	F 3	1979	105	1	0.995	1	0.0	0
Lake Haravattnet	F 4	1979	33	1	1	1	0	0
Lake Baulanjaure	H	1978	35	0.614	1	0.714	2.4	5.4
Small nameless lake close to but not connected with Lake Baulanjaure	H	1978	10	0.950	1	0.950	0.5	5.4
				$\chi^2_8 = 286.36$***		$\chi^2_8 = 192.26$***		

EST-2 locus, Nyman (1972) and Henricson and Nyman (1976) suggested that the complex population structure in Arctic char may be explained by the existence of at least three sibling species that evolved allopatrically during the last period of glaciation. Currently these sibling species occur sympatrically in some lakes, while incomplete isolation mechanisms resulted in introgression and loss of the original sibling species characteristics in other lakes. Henricson and Nyman (1976) also noted that the same sibling species pair is usually present within a whole river system, resulting in comparatively similar allele frequencies within the system.

The apparent allele frequency homogeneity among the *F 2–4* collection sites are in agreement with those observations. In contrast, the neighboring Lake Trollsvattnet (*F 1*), draining in another direction, exhibits dramatically different allele frequencies at *EST-2* ($P < 0.001$ as measured by Fisher's exact test). It should be noted, however, that these lakes (*F 1* on one hand and *F 2–4* on the other) belong to the same major drainage (River Indalsälven) where they meet some 100–150 km downstream. A similar phenomenon is observed in Lake Baulanjaure (H) and the neighboring lake located some 200 m from Lake Baulanjaure but draining in another direction. These lakes exhibit significant allele frequency differences at *EST-2* ($\chi_1^2 = 6.69$, $P < 0.01$) and the difference at *MDH-4* is also close to significance ($\chi_1^2 = 3.60$, $P < 0.06$). These two lakes drain into the same river (the upper part of River Indalsälven) where they meet not more than some 12–15 km downstream. These observations emphasize the significance of considerable genetic differences over small geographic areas.

Evolutionary Considerations

In contrast to the majority of previous electrophoretic studies on Scandinavian fish populations, we have scored a large number of loci, including those which were monomorphic in preliminary as well as in subsequent analyses. This approach permits the estimation of the amount of genetic divergence between populations (Nei and Roychoudhury 1974; Lewontin 1974; Nei 1975), as well as the construction of reasonably reliable dendrograms for the assessment of evolutionary relationships (Sneath and Sokal 1973; Nei 1981). Within each species the genetic relationships (as measured by Nei's (1975) gene identity (*I*)) have been summarized in such dendrograms using the unweighted pair group method of analysis (Sneath and Sokal 1973) for the natural populations where a minimum of 30 loci were analyzed (Fig. 3).

In brown trout there is a general tendency for closely located populations to cluster together and for populations from the same drainage to appear in the same major branch. However, there are several striking exceptions to this general trend. The geographically most closely located populations are those that occur sympatrically in Lake Bunnersjöarna (*I*), but the major branching point in the dendrogram is just between them. Further, the samples from the River Storån (*E*) drainage cluster in two distinct groups where Lake Boultenjaure (*E 3*) is found together with samples from the lower part of the system (*E 12–15*). These findings stress the need for a careful consideration of the possibility of gene flow discontinuities when attempting to define and identify distinct population segments (Utter 1980).

The Weichsel (*M*) stock derivatives were not included in the dendrogram because they do not represent naturally reproducing populations. This stock represents the only sample of anadromous brown trout which we have as yet examined; the other populations are all lacustrine. It is an interesting observation that no additional alleles at polymorphic or monomorphic loci were found in this stock, as compared to those already observed in the Swedish lacustrine samples. The average gene identity between the Weichsel derivatives and the other populations was 0.988. Additional anadromous populations must be examined for firm conclusions, but the present finding agrees with the results from rainbow trout (*Salmo gairdneri*) indicating that the anadromous behavior has evolved rather recently (Allendorf 1975; Allendorf and Utter 1979), and that apparent behavioral differences do not necessarily reflect a large amount of genetic divergence.

The same general tendency as found in brown trout is also observed in Atlantic salmon. Geographically close populations were more genetically similar than those further apart and tend to cluster in the dendrogram (Fig. 3). The major branching point in the dendrogram is between the two populations from the two small, more southern, lowland rivers (*C 5* and *6*) and the four other samples from the large mountain rivers (*C 1–4*) originating in the Arctic mountain areas. This might indicate the existence of an ecological basis for the pattern of genetic differentiation, but further samples are needed to settle this question.

The dendrogram constructed from Arctic char gene frequency data reveals quite a different pattern from that observed in the two other species as it exhibits only one significant branching point. Nyman (1972) and Henricson and Nyman (1976) suggested the existence of three sibling species of Arctic char in Scandinavia. Referring to unpublished data (1976) they concluded that one of those sibling species (named "F-tita" by the authors) is characterized by an *EST-2(100)* allele frequency of 0.98 (i.e. close to fixation) and that one of the other sibling species (normal char) is typified by the allele frequency 0.40. Several of our present sample sizes of Arctic char are small in size and were all collected over a comparatively restricted geographical area. The joint segregation pattern at *EST-2* and *MDH-4* is striking, however; both loci appear to be polymorphic in the same samples, and fixed or close to fixation for the common *100* allele in the rest of the samples (Table 3). Henricson and Nyman (1976) suggested the possible existence of five siblings species of Arctic char; the present data stress the need for surveys of a large number of loci in additional samples for further delineation of the evolutionary relationships within the *Salvelinus alpinus* species complex.

It has been suggested several times that the complex populations structure observed among Scandinavian salmonids may be explained by repeated advance and retreat of glaciation in the area (Child et al. 1976; Ferguson 1980; Nyman 1972; Henricson and Nyman 1976; Payne et al. 1971; Ryman et al. 1979; Svärdson 1979). Under certain assumptions, measures of genetic identity based on large numbers of randomly selected electrophoretic loci can be used for estimation of the time since divergence (Nei 1975). In Fig. 3 the time scale corresponding to the genetic identities of the dendrogram is also given. The last period of glaciation ended some 8000–10 000 years ago, and it is striking that almost all of the

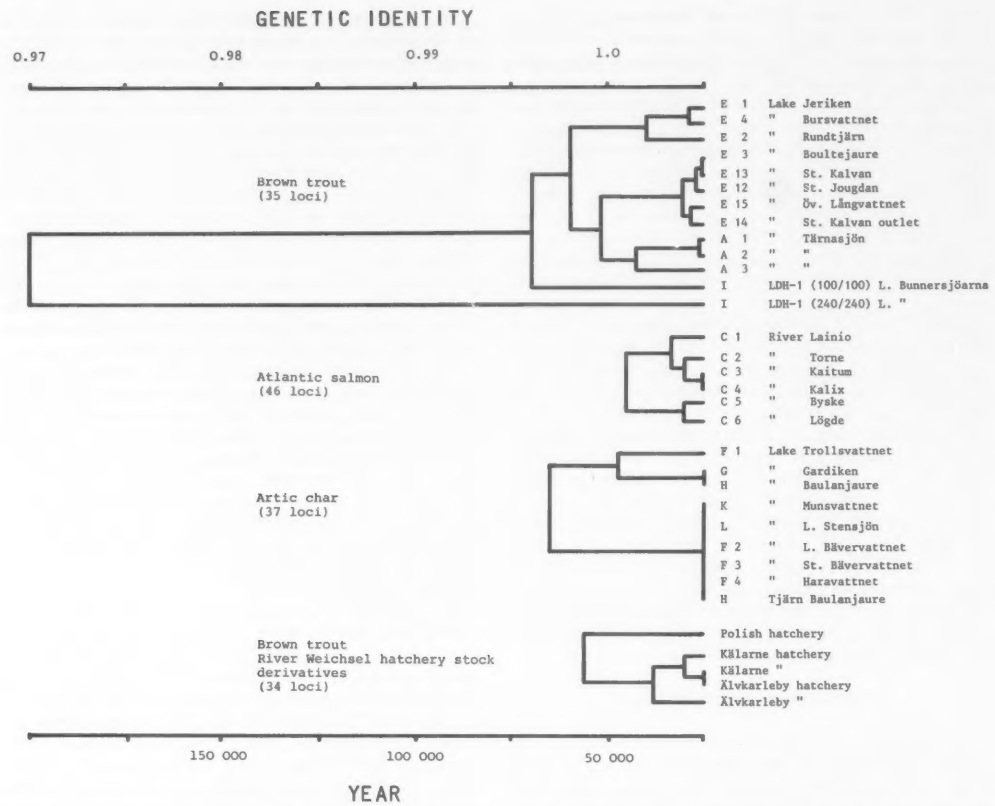

FIG. 3. Dendrograms (UPGMA, Sneath and Sokal 1973) summarizing the genetic relationships among populations of the three species investigated. (The dendrograms were constructed from gene identity (I) values (Nei 1975) based on the allele frequencies given in Tables 1–3.) Effective divergence time was estimated according to Nei (1975, p. 193).

branching points for the different species/populations are found after this geological event. Two brown trout populations of Lake Bunnersjöarna represent the only exception. The genetic identity between these two demes is actually larger ($I = 0.975$) than indicated in the dendrogram; they are both fixed for electrophoretically identical alleles at 19 additional loci not considered when constructing the present dendrogram to ensure that the identity values were computed using exactly the same loci in all populations. The estimated time of evolutionary isolation is 125 000 yr, which coincides with the beginning of the last period of glaciation in that area (Ryman et al. 1979). We do not question that the glaciations had a strong impact on the evolution of intraspecific forms within the salmonids, but the present data suggest that a considerable portion of the current substructuring has evolved subsequent to the periods of glaciation.

Hatchery Stocks

Many different factors such as overexploitation, hydroelectrical power, plant constructions, and acid precipitation have resulted in eradication of many salmonid stocks, and a large number of the remaining ones are threatened or endangered. This has necessitated the development of hatchery programs aimed at minimizing ecological and economical damage caused by drastic numerical reductions or complete elimination of numerous populations. In these cases the hatchery often functions as a gene bank, conserving and multiplying unique biological resources. It is of fundamental importance for the breeding program to prevent inadvertent damage of the gene pool through loss of genetically determined population characteristics.

In recent papers (Ryman and Ståhl 1980; Ryman 1981), we have presented evidence that current stocking procedures frequently may change the genetic composition of the stock that should be preserved. In particular, we stressed the need for using a large number of parents when founding and perpetuating the stock to avoid inbreeding and genetic drift. We also presented evidence indicating that occasionally the "wrong" stock was brought to the hatchery because of lack of information on the population structure and the amount of subdivision in the area where the parents were caught. We

present here some additional data indicating that current stocking procedures result in the loss of genetic variability and change of genetically determined population characteristics (see also Allendorf and Phelps 1980).

Anadromous brown trout stock from the Polish river Vistula (Map code *M*; river Weichsel on earlier maps) has long been famous for its fast growth rate and large body size. In the late 1950s, offspring from parents caught in river Vistula were brought to Sweden, and a stock named "Weichsel" was founded. The stock has since then (four to five generations) been continued through release of hatchery-reared fish followed by recapture and stripping of returning marked spawners (N. Steffner personal communication). Two different hatcheries (Kälarne and Älvkarleby) have been involved in the perpetuation of this stock, so there are two Swedish derivatives of it. The "Weichsel" stock is continued in a similar manner in Poland.

In 1979, samples from the various derivatives of the "Weichsel" stock became available for electrophoretic analysis through the kind cooperation of Mr. N. Steffner of the Älvkarleby hatchery in Sweden; the resulting allele frequencies are given in Table 1. There are highly significant allele frequency differences at all loci found to be polymorphic within this "stock." The major difference is between Polish stock on one hand and Swedish derivatives on the other (Table 1 and Fig. 3), but there are also highly significant differences at four of the five loci segregating in the Swedish subsets (sum of chi-square $\chi^2_{15} = 245.72$, $P < 0.001$). As indicated in Fig. 3, the amount of differentiation among the derivatives is comparable to that found among natural brown trout populations from different drainage systems.

Assuming that the original Vistula population was polymorphic at all six loci segregating in at least one of the present derivatives, the Polish stock appears to have lost half of these polymorphisms and one (17%) is no longer present among the Swedish subsets. Although the "Weichsel" stock appears to have lost a significant portion of its original genetic variability, it is still considered to represent a stock with comparatively good production characteristics. This might be due to the existence of a high level of genetic variability in the original population, permitting considerable loss of genetic variability before inbreeding depression can be detected. There is some support for such a hypothesis; if the original population was segregating at six loci, this would correspond to a proportion of polymorphic loci of 0.194, which is much higher than has been observed in a natural population of brown trout or any salmonid species in Scandinavia. The allele frequency differences observed within the "Weichsel" stock make it highly interesting for further studies aimed at estimating the amount of morphological, behavioral, and other phenotypic differences that might accompany the genetic ones.

Preliminary analysis of hatchery-reared Atlantic salmon indicates that genetic changes are induced during the stocking in this species also. Recently, spawners were collected in the River Lainio–Torne (*C 1* and *2*) drainage at Kukkola (*C 7*) and the Torne River mouth (*C 8*), with the intention of producing smolt for release to support the natural reproduction in this drainage. Allele frequencies at polymorphic loci among those hatchery-reared fish representing offspring from spawners collected in the field are given in Table 2. As pointed out previously, there is a significant difference between the *C 1* and *2* samples at *AAT-3*, indicating the possible existence of more than one population within the drainage. The *C 8* hatchery stock differs significantly from the *C 1* sample at *AAT-3* ($\chi^2_1 = 8.51$, $P < 0.01$) and both stocks differ from *C 2* at *SDH-1* (smallest $\chi^2_1 = 11.61$, $P < 0.001$). There is also a significant difference between *C 7* and *8* hatchery derivates at *PGM-1* (using Fisher's exact test $P \approx 0.01$). It is not clear whether these differences reflect the sampling of two few spawners (founder effect/genetic drift), the existence of additional populations within the drainage, or the inclusion among the parents of strayers actually belonging to other rivers. At any rate, there appears to be an obvious risk that the hatchery fish represent offspring from forced matings between different populations that might result in a breakdown of reproductive barriers and adverse mixing of locally adapted gene pools.

At present, it is not possible to determine the causes for the hatchery-stock allele frequency heterogeneities previously presented (Ryman and Ståhl 1980; Ryman 1981) and in this paper. However, on the basis of our general knowledge of Scandinavian hatchery-breeding procedures, we feel that a considerable portion of the intra-stock heterogeneities might well be explained by genetic drift, and founder effects induced by the use of too few parents in the founding and perpetuation of the stocks (Ryman and Ståhl 1980). There is an urgent need for more detailed studies of these phenomena to elucidate their causes and biological significance, as well as for continued surveillance of the genetic composition of hatchery stocks.

Genetic Effects of Release of Hatchery Fish

The results presented in the first section of this paper referred to natural populations which largely, with the exception of continuous harvest, have been undisturbed by planting, damming, or similar perturbations. The pattern of genetic variation observed among these populations must therefore be assumed to reflect a natural state with regard to the population structure and distribution of genetic variation. Possible differences between that pattern and the one observed among manipulated populations would indicate how genetic resources are influenced by human activities.

We have brown trout data from one area, the River Skellefteälven drainage (*D*) in northern Sweden, that could serve the purpose of such a comparison. There are several water reservoir and dam constructions along the River Skellefteälven; to compensate for the resulting damage on natural brown trout populations, hatchery fish of various origins have been successively planted for a long period of time. Samples from widely separated locations (Fig. 1D) were collected for electrophoretic analysis by electroshocking. All the fish were so young (less than 2 yr) that it was clear that they did not represent planted hatchery fish; they were all the result of natural reproduction in this drainage.

The gene frequency distribution among these samples (*D 1–3*) is given in Table 1. Although the sampling locations were distributed over a wide geographic area, there are no significant gene frequency differences among the samples except for *PGI-3* ($\chi^2_2 = 6.89$, $P < 0.05$). However, this is a "weak" significance because the allele frequencies are so

skewed that the underlying assumptions for the χ^2 heterogeneity test is violated by small expected values. Further, there is no indication of an overall heterogeneity as judged from the sum of chi squares ($\chi^2_{10} = 16.98$, $P > 0.05$). As a matter of fact the allele frequencies are surprisingly similar as compared to the differences typically obtained among collections from undisturbed populations over much smaller geographical distances (Fig. 1, Table 1).

Although this lack of observable heterogeneity among the samples is striking, it must be remembered that the absence of statistical significance alone is not really informative. However, analysis of the genotypic distribution at *AGP-2* provides additional and much stronger evidence of an unnatural genetic composition of these populations. The genotypic distribution at *AGP-2* is (94; 56; 0) of the three genotypes *100/100*. *100/50*, and *50/50*, respectively. The total absence of *50/50* homozygotes is highly conspicuous, and altogether there is a highly significant heterozygote excess ($\chi^2_1 = 7.73$, $P < 0.01$) which is consistent among all three samples. A similar but not as conspicuous and statistically insignificant excess of heterozygotes is also found at *MDH-2*, the other locus permitting a comparison with Hardy–Weinberg expectations in this sampling area: the sum of these two chi squares is also significant ($\chi^2_2 = 8.92$, $P < 0.05$).

We have analyzed the genotypic distribution at *AGP-2* in well over 100 undisturbed natural populations of brown trout, but have never observed significant excess of heterozygotes. Crosses between genetically distinct populations are expected to result in excess of heterozygotes. The present results strongly suggest that previously existing reproductive barriers between natural populations inhabiting the River Skellefteälven have been broken down and resulted in forced matings between previously existing genetically distinct populations. The genetic characteristics of these subpopulations have most likely been lost.

Conclusions

Genetic variation in natural populations constitutes a biological resource that must be properly managed so as not to reduce future opportunities for use of the resource. In brown trout, a large fraction of the genetic variation appears to be distributed among populations, and existing data indicate that this may be true in other salmonids and closely related species also (Nyman 1972; Kirkpatrick and Selander 1979; Svärdson 1979; this paper). There is a general concern about man's impact on natural populations, and the present data clearly indicate that currently practiced exploitation and management activities may easily reduce the genetic variability among and within natural and hatchery populations.

A large number of valuable populations have been and are continuously being lost as a result of habitat destruction and unwise management programs. The continuously increasing exploitation of land and water resources calls for immediate identification of the genetic resources that are still present in natural populations. It is recognized that it would be impossible to conserve all the genetic variability that is currently existing among natural populations. Decisions concerning the amount of effort that should be spent on conservation activities of single stocks must be based on a thorough description of the genetical and ecological characteristics of each particular population. A detailed survey of the amount of genetic diversity that is still present among natural populations appears to be the most urgent prerequisite for proper decisions about further conservation activities. Such a survey must be carried out over as wide geographical range of environmental conditions as possible and should preferably be accomplished on an international basis.

Gene bank or stocking programs should normally be started after detailed analysis of the genetic structure of the populations involved. Continuous surveillance of the genetic composition of hatchery stocks should be maintained. A detailed understanding of the reproductive relationships within the species is a basic requisite for formulation of effective management programs. Electrophoresis provides a reliable tool in delineating the variability and differentiation of gene pools, and an extensive use of such techniques in the planning and carrying out of sound fishery management programs is foreseen.

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Stocks of Atlantic Salmon (*Salmo salar*) in Britain and Ireland: Discreteness, and Current Management[1,2]

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The null hypothesis that all Atlantic salmon (*Salmo salar*) in the North Atlantic belong to a common stock is shown to be untenable, on the grounds of differences between North American and European populations in transferrin gene frequencies, chromosome numbers, and numbers of circuli on scales. The further hierarchical breakdown of the European fraction into western, northern, and Baltic components is revealed through tagging data, which also shows distinctions within the western group, segregating into Icelandic, French, and British/Irish subpopulations. Within the latter, two groups are definable on the basis of differences in transferrin (Tf_2) gene frequencies, the boreal and celtic races. Within the celtic race, the populations of the neighboring rivers Bandon and Blackwater (Cork) have been shown to be distinct reproductively isolated stocks, on the basis of differences in gene frequencies in two enzymes (IDH-A, and AAT-A). Circumstantial evidence for the separate identity of 74 river stocks in Britain and Ireland, on the basis of differences in age structure at the smolt and adult stage, and size at return to the rivers, is supported by evidence from tagging experiments of a high incidence of homing to the native river, experimental evidence of the heritability of growth and developmental traits, and evidence from scale data of differences in specific growth rate of individual river populations during their 1st year at sea. Environmental pressures selecting for differences between river stocks are suggested by the significant positive correlation between river length and fish size at maturity. Differences in patterns of change in the commercial catch over the period 1952–76 indicate regional groups of river stocks within Scotland. The existence of such discrete stocks of Atlantic salmon implies the need for management on a stock-by-stock basis. Current national and international regulations do not achieve this goal.

Key words: Atlantic salmon, transferrin gene frequencies, river stocks, management

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Nous démontrons que l'hypothèse nulle à l'effet que tous les *Salmo salar* de l'Atlantique nord sont membres d'un même stock ne tient pas. Nous nous basons sur des différences entre populations nord-américaines et européennes dans la fréquence génique de la transferrine, le nombre de chromosomes et le nombre de circuli sur les écailles. De plus, les résultats de l'étiquetage montrent que la fraction européenne peut se subdiviser en composants ouest, nord et baltique. Ils montrent également des distinctions parmi le groupe de l'ouest, soit des sous-populations islandaise, française et britannique/irlandaise. Chez cette dernière, on peut encore définir deux groupes, selon la fréquence génique de la transferrine (Tf_2) : les races boréale et celtique. On a démontré, au sein de la race celtique, en se basant sur des différences de fréquence génique dans deux enzymes (IDH-A et AAT-A), que les populations des rivières Bandon et Blackwater (Cork) voisines constituaient des stocks sexuellement isolés. Les preuves indirectes de l'identité distincte de 74 stocks fluviatiles en Grande-Bretagne et en Irlande, soit les différences dans la composition par âge aux stades de smolts et d'adultes, et

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[2]Tabular material and references are available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Canada, K1A 0S2.

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la taille au moment du retour en rivière, sont appuyées par des expériences d'étiquetage au cours desquelles il y eut forte incidence de retours à la rivière natale, par des preuves expérimentales de la transmission héréditaire des caractéristiques de croissance et de développement, et enfin par des preuves, fournies par les écailles, de différences dans le taux de croissance spécifique de populations de rivières individuelles durant la première année en mer. La corrélation positive significative entre la longueur en rivière et la taille du poisson à maturité donne à penser que l'environnement exerce des pressions résultant, par sélection, en des différences entre stocks fluviatiles. Les changements différents qui se sont produits dans les prises commerciales durant la période 1952–76 indiquent qu'il existe des groupes régionaux parmi les stocks fluviatiles d'Écosse. L'existence de stocks de saumons atlantiques distincts comporte la nécessité d'une gestion par stocks individuels. La règlementation nationale et internationale n'atteint pas cet objectif.

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MENZIES' account (in Moulton 1939) of local stocks of Atlantic salmon (*Salmo salar*) was based chiefly on extensive scale-reading studies carried out by himself and his colleagues in Scotland over the previous 30 years. Since that time more data have become available on these and other populations throughout the United Kingdom, and Ireland, together with information on homing, biochemical distinctions between populations over wide areas, and developmental physiology of the species. The present paper reviews the evidence for the existence of discrete stocks of Atlantic salmon in the British Isles, and the extent to which current management takes stock structure into account.

The 1938 Ottawa conference (Moulton 1939) recommended that "the term *stock* should be used to describe fish spawning in a particular lake or stream at a particular season, which fish did not interbreed with any group spawning in a different place, or in the same place at a different season." Information available from the rivers of Britain and Ireland is as yet insufficient to distinguish such stocks within rivers, and therefore in the present paper stocks are equivalent to the whole populations of specific rivers.

Background

DISTRIBUTION OF THE SPECIES

Atlantic salmon are distributed throughout the North Atlantic area, reproducing in rivers from latitude 43°N to 59°N on the east coast of North America, in Greenland, in Iceland, along the western and northern coasts of Europe from latitude 43°N to 71°N, and in arctic Russia as far east as the Kara River (MacCrimmon and Gots 1979). Landlocked populations exist on both sides of the Atlantic, but the vast majority of juvenile salmon enter the sea at a length of 10–20 cm, in the late spring of their 2nd–6th years, spending 1–5 years there before returning to reproduce in freshwater. During that period their weight increases by about 100 times. Little is known in detail of their distribution at sea, but by marking juvenile downstream migrants, it has been shown (Jensen 1980a; Ruggles and Ritter 1980; Swain 1980) that individuals originating from many localities in both Europe and North America intermingle on feeding grounds to the west, south, and southeast of Greenland. Several other feeding areas have been identified, notably off the east coast of Newfoundland where individuals derived from many Canadian rivers have been caught; off the north Norwegian coast, where individuals from a range of northern European rivers have been taken; around the Faroe Islands (62°N 7°W), where fish marked in British, Irish, Icelandic, and Scandinavian rivers have been found; and off the west coast of Ireland, where salmon from a wide range of British and Irish rivers have been caught. Partially enclosed sea areas, such as the Bay of Fundy and the Baltic Sea, provide marine feeding grounds for salmon from rivers discharging into them.

DISTRIBUTION OF STOCKS

In view of such intermingling of fish of widely differing geographical origin, and the suggested marine origin of the salmonid fishes (Calderwood 1941), it is convenient to begin considering the question of stocks by taking as a null hypothesis the statement: all Atlantic salmon in the sea form a single common stock.

Distinctions between American and European salmon — Recent work on protein polymorphisms, on chromosome number and structure, on scale characteristics, and on parasites has shown that differences exist between fish of European and North American origin found in the common feeding areas off Greenland. In the 1960s Nyman (1966, 1967) had shown differences in serum and tissue proteins and esterases between Swedish and Canadian salmon. Payne et al. (1971) then found that the transferrin alleles Tf_3 and Tf_4 occur in salmon in North American but not in European rivers, and that allele Tf_2 occurs in European and not in American rivers. Both alleles are present among fish in Greenland. If the movement of adult salmon from the sea into freshwater to spawn were a purely random process, then the Greenland Sea feeding population should be scattered at random as mature adults in American as well as in European rivers. The association of separate distinct transferrin alleles with the separate continents is evidence of the segregation of distinct continental portions of the North Atlantic feeding population of salmon.

Boothroyd (1957, 1958, 1959) has shown that the distribution of cytological types differs between salmon from American and European rivers, and has postulated that the diploid number of 56 in North America has been evolved through two centric fusions or misdivisions from that of 60 in European

salmon. However, Grammeltvedt (1975) found diploid numbers ranging from 55 to 60 (maximum at 58) in Norwegian salmon, in agreement with the findings of Rees (1967) and Nygren et al (1968, 1972), also on European salmon.

K. Mosher (1973, unpublished data) counted the circuli in the first ocean growth zone of scales from adult Atlantic salmon caught in their home-water regions. While the total frequency distributions of circuli from the various regions overlap, his data suggested distinct regional differences. Lear and Sandeman (1980) extended this approach, and using a number of discriminant functions incorporating circuli counts from the second river zone and the width of first sea zone, in addition to circuli counts of the first sea zone, they were able to separate American from European salmon with 85.6–93.6% efficiency.

Pippy (1969, 1980) found the Ancanthocephalan parasite *Pomphorynchus laevis* in smolts from the British Isles, but not in North American smolts, and the parasitic copepod *Salmincola salmoneus* on the gills of Canadian smolts, but not on European ones. Although these parasites have separate geographic distributions, their use as indicators of stock distinction in their hosts is not conclusive, as neither species was on salmon in the Greenland fishery samples. However, the mean number of larvae of the nematode *Anisakis simplex* per salmon host was found to be greater among European salmon than among American salmon (Beverley-Burton and Pippy 1978).

The first step in the hierarchical rejection of the null hypothesis can therefore be taken: American and European Atlantic salmon form distinct non-interbreeding subpopulations within the species. Further subdivision of the American fraction has been considered by other authors (Power, Saunders) at this symposium.

Regional groupings within Europe — Within the European segment of the West Greenland salmon population, individuals have been taken marked as juveniles in France, Ireland, United Kingdom, Iceland, Norway, and Sweden (Swain 1980). However, the proportions of these tag recoveries, in relation to the numbers of smolts tagged in the respective countries, are not uniform, which suggests that, providing the tagging process was equally efficient at all marking sites, the Greenland feeding population is not a completely random representation of salmon from all Europe's producer streams, but a limited mixture drawn predominantly from France, Ireland, and Britain. Similarly, as relatively few tagged fish of Scandinavian origin have occurred in the Greenland fishery, relatively few of French, Irish, British, Icelandic, or Baltic origin have been taken in the Lofoten fishery, and none other than fish of Baltic origin in the Baltic fishery.

Conversely, feeding fish tagged and released in Greenland waters have been recaptured in home-water fisheries of various European countries (Jensen 1980b). As with the recoveries in Greenland of fish tagged as smolts, so with fish tagged in Greenland, recoveries as 2-sea-winter and older adults as a proportion of total catches of these age-groups in home waters differ between individual European countries. Again, these recoveries suggest a closer link between the Greenland Sea population and the more westerly European rivers, than the more northerly and easterly ones.

Evidence of differences in protein polymorphisms among these major European subdivisions is lacking as yet, but new enzyme markers are being studied (Child 1980). Data from scale pattern analysis support the link between Greenland and the westerly European rivers (K. Mosher unpublished data). The fact that a few Scandinavian smolts have appeared later among the Greenland catch, and that a few tagged adults from the Greenland feeding grounds have been recovered in Scandinavia, suggests the isolation of supposed regional populations from western and northern Europe is incomplete. This conclusion is reinforced by the marking experiments of Dahl (1938) and Menzies (1937, 1939), who recorded movements of tagged adult salmon from the coasts of Scotland to Norway and vice versa, and more recent recoveries in Norway and the U.S.S.R. of salmon marked as smolts in Scotland (Shearer personal communication); in Ireland of salmon tagged as smolts in Norway, Sweden, and Denmark (Went 1973b); and in Sweden of a salmon marked as an adult on the Irish coast (Went 1973b). However, these movement data are isolated instances, and account for a tiny fraction of all recoveries during such marking experiments.

Accepting that there may be some limited overlap in the ambit of the northern and western components of the European salmon population, marking evidence is consistent with the existence of such definable components. Concentrating on the western subpopulation, salmon marked as smolts in Iceland have been recaptured only as adults in Iceland, off Greenland, or in Faroese waters (Isaksson 1980). Furthermore, no adults of known British, Irish, or French origin have been taken in Iceland. However, salmon tagged as smolts in Britain and Ireland have been taken in the drift-net fishery off Donegal and off other parts of the western coast of Ireland (Went 1973b). A higher proportion of tagged French salmon has been caught in Greenland than in home waters in France (Swain 1980), but no recoveries have been reported from the Irish fishery. Hence, the Icelandic and French salmon may be regarded on circumstantial evidence only, as separate subpopulations, but the Irish and British salmon, mixing in a second area, may be less clearly separable.

Some adult fish marked off the west coast of Scotland (Menzies 1938b) were recovered in Irish waters, so that it is pertinent to consider the salmon populations of the whole of the British Isles together.

Salmon Populations of Britain and Ireland

Biochemical Genetic Differences

Payne et al. (1971) examined the frequency of the Tf_2 gene among samples of salmon taken from a range of rivers all around the coasts of Britain and Ireland, and as a result proposed the existence of two genetically distinct races of salmon in Britain, the Celtic and the Boreal (Fig. 1) (Payne et al. 1971, Child et al. 1976). These authors proposed that the two races originated as a result of glacial changes in the Pleistocene era. The Boreal race may have been isolated for 15 000 years in the North Sea (Rhine Sea) at the time of the Wurm 3 glaciation, and then recolonized Scotland and Ireland with the retreat of the glaciers. The Celtic race may have remained in the south and southwest region where its present boundaries, east and west, coincide with terminal moraines of the glaciation. During the period of isolation of the two races, a land bridge existed between Britain and Europe across the

FIG. 1. Tf_2 allele frequencies among river populations of Atlantic salmon in Britain and Ireland. (From Payne et al. 1971.) Stippled area shows range of "celtic" race.

eastern end of the English Channel. With separation after the Wurm 3 period, the Boreal race could have colonized westward, thus accounting for the presence of such fish in the modern rivers of Avon and Stour.

Cross et al. (1978) found significant differences in the gene frequencies at the isocitrate dehydrogenase-A (IDH-A) and aspartate aminotransferase (AAT-A) loci, in juvenile salmon from the Blackwater and Bandon rivers of southern Ireland, which are only 80 km apart at their mouths. These gene frequencies at both loci in Blackwater juveniles were similar to those for Blackwater adults recorded by Cross and Payne (1977) and Payne and Cross (1977). They concluded that these river populations were reproductively isolated, and should be treated as distinct stocks. These then form a further stock subdivision among the celtic race defined by Payne et al. 1971, and Child et al. 1976.

TABLE 1. Rank correlation coefficients of angling

Group	River	1	2	3	4	5	6	7	8	9
1	1. Tweed		0.576	0.854	0.712	0.615	0.390	0.578	−0.293	0.103
	2. South Esk			0.535	0.373	0.276	0.033	0.368	−0.037	0.005
	3. Dee (Aberdeenshire)				0.783	0.026	0.455	0.562	−0.508	0.053
	4. Don					0.703	0.484	0.440	−0.657	−0.237
	5. Deveron						0.747	0.702	−0.290	0.264
	6. Beauly							0.487	−0.397	0.164
	7. Awe								−0.311	0.106
2	8. Tay									0.548
	9. Findhorn									
	10. Ness									
	11. Conon									
	12. Kyle									
	13. Helmsdale									
	14. Thurso									
	15. Naver									
	16. Loch Roag									
	17. Clyde									
	18. Girvan									
	19. Nith									
	20. Spey									

[a](—) Correlation positively or negatively significant, respectively, at the 99% level; (- - -) correlation positively or negatively significant,

Other divisions of the salmon of the British Isles based on their parasites were proposed by Beverley-Burton and Pippy (1978), who found mean values of 14.2 larval *Anisakis simplex* per 2-sea-winter salmon host examined from Scotland, as compared with 6.1 for Irish and 6.0 for English salmon. Their conclusion that the host fish had fed in different marine areas was supported by the frequencies of acid phosphatase phenotypes found among the nematode larvae, being in Hardy–Weinberg equilibrium among the Scottish hosts, but not so among the English and Irish (Beverley-Burton 1978).

Child (1980) reviewed exploratory work on the enzyme systems in salmon sera. The most promising enzyme for use as a genetic marker was glucose-6-phosphate isomerase (GPI), which showed a number of variants of the anodal homodimer GPI-A in salmon of some Scottish rivers.

DIFFERENCES IN PATTERN OF CATCH

Data on angling catches over the 25 years (1952–76) give evidence of regional grouping of river populations of salmon in Scotland. For 20 rivers with catches consistently greater than 1000 fish per annum, total catches were ranked by years from lowest to highest, and rank correlation coefficients calculated for all pairs of rivers in turn (Table 1). On the basis of the statistical significance of these correlations, the patterns of change from year to year in catches showed two major groupings of rivers (Table 1). These represent two geographical regions, group 1 consisting of the east coast rivers from the Tweed to the Deveron, and group 2 the Moray Firth and north coast rivers (see Fig. 2 for geographical locations). The correspondence is not perfect, as geographically the Tay falls in group 1, and the Beauly in group 2. When the nature of the changes occurring during these 25 years was examined further, the following patterns were found: group 1: 1952–56: catches at average level, 1957–66: catches at high level, 1967–76: catches at low level; group 2: 1952–61: catches at low level, 1962–76: catches at high level. In group 1, the decline in numbers of fish of the older sea-age groups, probably as a consequence both of open sea fisheries (see Parrish and Horsted 1980) and environmental changes in the North Atlantic, affecting growth, survival, and maturation timing (Martin and Mitchell unpublished data), offset the increases in 1-sea-winter fish recorded generally in the 1960s and 1970s. In group 2 there was no comparable decline in the older sea-age groups, and the rise in catches started 5 years later than in group 1. Plots of the cumulative sums of deviations from the 25-yr mean catch values for these two groups (Ewan 1963; Woodward and Goldsmith 1964; Mitchell 1978) illustrate these differences in pattern of change (Fig. 3). The regional nature of these groupings, although not perfect, suggests that populations of salmon from groups of rivers are behaving similarly at sea, but that difference in behavior between groups is also occurring.

DIFFERENCES IN GROWTH AND MATURATION RATES

All other descriptions of individual river populations of salmon in Britain and Ireland have relied upon age composition of the smolt runs and of the returning adults, size at the end of each successive winter of life, size at the return to the river, season of return, frequency of spawning, and some morphological measurements. Data on a number of these characteristics for salmon populations of 74 rivers in Scotland, Ireland, England, and Wales have been summarized from the literature and transferred to the Depository of Unpublished Data at the National Research Council of Canada in Ottawa. Each characteristic is considered separately below. Determinations of age and length at age were made in all cases from scales taken from adult fish caught entering the river system named. As most samples were taken

catch in 20 Scottish rivers over 25 years 1952–76.[a]

10	11	12	13	14	15	16	17	18	19	20
0.134	0.062	−0.160	−0.063	0.434	0.030	0.150	0.059	0.372	0.533	0.281
0.202	0.217	0.051	0.321	0.282	0.212	0.158	0.385	0.604	0.471	0.145
0.115	0.020	−0.222	0.047	0.073	−0.088	0.108	0.017	0.234	0.215	0.258
−0.342	0.287	−0.311	−0.273	0.072	−0.158	−0.161	−0.098	0.126	0.145	0.180
0.024	0.141	0.013	0.057	0.292	0.065	0.169	0.102	0.265	0.297	0.315
0.003	0.276	−0.140	0.022	0.119	0.003	0.223	0.171	0.164	−0.003	0.043
0.123	0.183	0.205	0.098	0.394	0.194	0.402	0.325	0.594	0.287	0.009
0.686	0.459	0.490	−0.505	0.222	0.426	0.248	0.155	0.021	0.364	0.139
0.602	0.447	0.295	0.422	0.284	0.288	0.269	0.017	0.142	0.345	0.292
	0.635	0.503	0.708	0.490	0.467	0.594	0.336	0.276	0.606	0.214
		0.307	0.464	0.635	0.599	0.735	0.625	0.345	0.365	−0.009
			0.487	0.363	0.527	0.386	0.273	0.210	0.307	0.309
				0.314	0.218	0.512	0.231	0.257	0.396	0.349
					0.660	0.609	0.427	0.300	0.643	0.197
						0.565	0.684	0.361	0.365	−0.001
							0.543	0.428	0.411	−0.063
								0.645	0.218	−0.388
									0.459	−0.259
										0.220

respectively, at the 95% level.

from net fisheries, subject to statutory limitation of fishing seasons, the samples represented the catchable part of the river population in each case, and not the total population. Furthermore, the samples were taken over a total period of 71 years (1908–78) during which there have been major changes in the international exploitation of salmon, which have probably led to changes in age structure of the populations generally. Therefore comparisons between data for different rivers should be considered with caution, and due attention paid to the dates when these measurements were made. Nevertheless certain features are sufficiently clear to warrant further discussion.

In general, if the maturing population of salmon in the sea is a random mixture of contributions from all the rivers producing smolts, and if at maturation these adults move at random into those rivers to spawn, then each river should receive a population of adults which is a random sample of all the maturing fish at sea. Menzies (1937, 1938a) marked 1703 adult salmon caught at a coastal net station, away from a river mouth, at Loch Inchard, Scotland (Fig. 2), during 1936 and 1937, and recorded 205 recoveries from 240 km south to 660 km east and south. Hartley (1938) analyzed the growth patterns from scales of 1240 of these salmon caught at Loch Inchard during the 1937 experiment. In contrast to studies made from individual river-mouth samples, he found that these fish showed a wide range of growth patterns.

The length–frequency distribution of the smolts was asymmetric, and ranged from 6 to 17 cm, characteristic of the entire Scottish population rather than that of an individual river. Mean length of fish at the formation of the first sea annulus was less than 50 cm, which was then more typical of fish entering east coast than west coast rivers. While Menzies' data on distribution and numbers of marked salmon recovered do not make allowances for differences of netting effort to the south and to the east of Loch Inchard, the combination of information on recovery site and growth history does suggest a mixed population off northwest Scotland with a preponderance of fish showing freshwater characteristics of non-northwest coast river origin. Consequently in a restricted geographical area such as the British Isles, where the opportunity for salmon from all parts to mix at sea has been demonstrated, it would be expected that size and age structures of the populations sampled from net catches at the different river mouths would be the same, within the limits of sampling error. The deposited data show that this is not the case.

Growth rate in freshwater and thus the age at which smolts leave the rivers is dependent inter alia on the productive capacity of those rivers and their temperature regimes. Therefore it would be expected that the age composition of the smolt runs from different rivers would differ, but that if the migrants intermingled at sea, the smolt-age composition of the adult populations sampled by the net fisheries in those river mouths would not differ. That they do differ is evidence of nonrandom segregation of the marine stock on reentry to the rivers.

Age and size at maturity in Atlantic salmon have been shown to be influenced strongly by environmental factors (Martin and Mitchell unpublished data), as in the experiments of White and Huntsman (1938), who showed that the progeny of characteristically large, long-sea-absence fish of the Restigouche River, New Brunswick, when reared in the Apple River, Nova Scotia, returned as small 1-sea-winter fish, characteristic of the salmon native to that area. It would therefore be expected that, even if the rivers over the whole of the British Isles did not show a uniform picture of adult age and size structure, at least neighboring ones would. Even this is not the case (Table 2). Three pairs of rivers have been examined closely (see Fig. 2 for geographical locations): the Test and Itchen drain into a common estuary on the south coast of England, the Usk and Wye discharge into the Severn Estuary

FIG. 2. Rivers and lochs mentioned in text and tables. SCOTLAND: 1, Tweed; 2, Forth; 3, Tay; 4, Almond; 5, Tummel; 6, South Esk; 7, North Esk; 8, Dee (Aberdeen); 9, Girnock; 10, Don; 11, Deveron; 12, Spey; 13, Findhorn; 14, Ness; 15, Beauly; 16, Conon; 17, Kyle; 18, Helmsdale; 19, Thurso; 20, Naver; 21, Hope; 22, Loch Inchard; 23, Grimersta; 24, Loch Roag; 25, Morsgail; 26, Uig; 27, Laxdale; 28, North Harris; 29, Ullapool; 30, Ewe; 31, Balgy; 32, Loch Shiel; 33, Loch Awe; 34, Clyde; 35, Girvan; 36, Dee (Kirkcudbright); 37, Nith; A, Moray Firth; B, Solway Firth. IRELAND: 1, Bush; 2, Bann; 3, Roe; 4, Foyle; 5, Finn; 6, Erne; 7, Bundrowes; 8, Drumcliffe; 9, Sligo; 10, Ballisodare; 11, Moy; 12, L. Carrowmore; 13, Owenmore; 14, Owenduff; 15, Burrishoole; 16, Corrib; 17, Shannon; 18, Feale; 19, Laune; 20, Inny; 21, Waterville; 22, Blackwater (Kerry); 23, Bandon; 24, Lee; 25, Blackwater (Cork); 26, Liffey; 27, Boyne. ENGLAND AND WALES: 1, Esk; 2, Tyne; 3, Derwent; 4, Duddon; 5, Leven; 6, Kent; 7, Lune; 8, Wyre; 9, Hodder; 10, Ribble; 11, Dee (Cheshire); 12, Usk; 13, Wye; 14, Severn; 15, Taw; 16, Torridge; 17, Camel; 18, Fowey; 19, Lynher; 20, Tamar; 21, Tavy; 22, Axe; 23, Stour; 24, Avon; 25, Test; 26, Itchen.

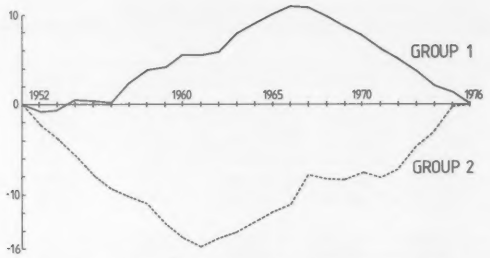

FIG. 3. Cusum plots of total catches of Atlantic salmon from 1952 to 1976, for two groups of Scottish rivers (see text).

within 30 km of each other, and the Finn is a tributary of the Foyle in the northwest of Ireland. In each case the age composition of adults entering the rivers in the same year has been consistently and significantly different ($P < 0.001$) over periods of 5, 9, and 19 years, respectively.

Menzies (1923) attempted to distinguish salmon from the River Dee (Aberdeen) and the River Spey using several measurements of body size and proportion among fish sampled from the net catch at the mouths of these rivers. He concluded that these data provided sufficient evidence "to establish the existence of separate races of salmon in these rivers." Much of his information is not susceptible to adequate statistical analysis. However, his data on weights of fish show that those entering the Spey are consistently heavier than those entering the Dee, over all age-groups and months of the year ($P < 0.001$), and that Spey entrants are also consistently heavier at any given length than Dee entrants ($P < 0.001$).

In Fig. 4 the mean weights of salmon in the net catches of 1952–76 from 26 Scottish rivers are plotted against river length. The positive correlation is highly significant ($P < 0.001$) suggesting a selection pressure for increased adult size with increased energetic demand at the end of their spawning migration (Foerster 1968). Schaffer and Elson (1975) plotted mean weight of rod-caught salmon against the river length for five regions of eastern Canada and found significant increases in fish size with the river length in three of these, a positive but not significant correlation in 1, and no correlation at all in another. The absence of statistically defin-

TABLE 2. Age composition of adult salmon entering pairs of neighboring rivers.

Rivers	Years		Sea-age-group percentages 1	2	3	4	Previous Spawners	Authority
Test	1966–70		6.4	49.1	40.0	0.7	3.8	Anon. 1967–71
Itchen	1966–70		15.4	62.0	18.0	0.3	4.3	Anon. 1967–71
		Differences χ^2	12.3	24.8	673.7	—	0.9	
		P	<0.02	<0.001	<0.001	—	n.s.	
Usk	1965–73		18.9	53.2	24.8	1.8	1.2	Anon. 1966–74
Wye	1965–73		12.6	41.0	43.6	1.3	1.5	Staite 1967–74
		Differences χ^2	123.4	186.5	69.4	23.8	15.7	
		P	<0.001	<0.001	<0.001	<0.01	<0.05	
Foyle	1954–71	Means	89.8	7.2	—	—	3.0	
		Ranges	79.7–97.2	0.8–14.3	—	—	0.3–8.0	Went 1972
Finn	1954–72	Means	18.7	78.4	—	—	2.9	Went 1973a

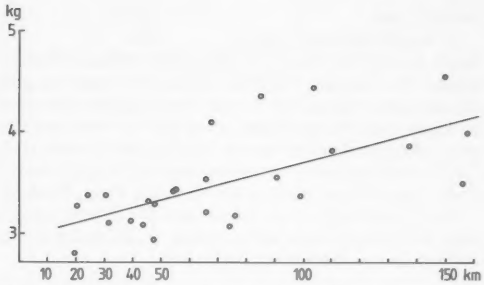

FIG. 4. Regression of mean weight of adult Atlantic salmon caught in commercial nets, on river length, for 26 Scottish rivers.

able relationships in these latter areas was considered attributable in part to the selective removal of larger salmon by fisheries. Despite similar recent reductions in the number and proportion of older larger fish in the catches in Scottish rivers (e.g. Tay and Spey), the fish–size to river–length relationship is still evident, indicating real differences in growth and maturation characteristics of individual river stocks.

TIMING OF UPSTREAM MIGRATION

Most authors of papers detailing the characteristics of salmon in specific rivers of the British Isles have also noted the seasonal distribution of the catches. Many consider that the timing of these runs is itself a distinctive racial characteristic, but Nordqvist (1906, 1924) reviewed this subject over the entire geographical range of Atlantic salmon and concluded that the seasonality of such runs was determined by local hydrological factors at least for fish in the length range 70–90 cm. He showed that for very large salmon (>100 cm long, usually aged 3 sea winters or more), entry to rivers was often about 1 year prior to spawning, and might be even earlier in rivers where ice conditions made entry impossible later, as, for example, in Arctic Russia. He suggested that in rivers where there were seasonal difficulties associated with upriver migration, entry time of fish would be evolutionarily adjusted to ensure that adult salmon were in the right place at the right time to overcome obstacles and reach the spawning grounds (cf. Seligo 1896, 1925; Hoek 1910).

British rivers are relatively small and short, and while such finely tuned evolutionary adaptations may well exist in the salmon populations of these islands as suggested above (Differences in Growth and Maturation Rates section and Fig. 4), they have yet to be demonstrated conclusively.

As noted earlier, White and Huntsman (1938) showed that salmon originating from the Restigouche River, transplanted to the Apple River, migrated into the latter river at a time similar to locally native salmon and dissimilar to that of their parental Restigouche population.

FECUNDITY DIFFERENCES

Pope et al. (1961) sampled adult female salmon from six rivers in Scotland, determining the exponential relationships between egg number and length for each population, over 3 successive years. By comparison of the linear regressions of log egg number on log length, they showed that year-to-year variation occurred in each river, but was insignificant, while significant differences ($P < 0.01$) occurred between rivers.

Aulstad and Gjedrem (1973) found differences in egg size of salmon from different regions in Norway, and Larsson and Pickova (1978) found that eggs of 3-sea-winter salmon from the Umeälv, Sweden, were significantly smaller than those of fish of comparable age from the neighboring rivers Luleälv and Skellefteälv.

TABLE 3. North Esk River: Percentage[a] age-composition of smolt run and of adults returning from it: average for the 15 smolt years 1961–77.[b]

Freshwater years	1	2	3	4
As smolts	5.50	65.81	27.45	1.23
As returning adults	1.79	61.29	33.40	1.21
Differences	$P<0.001$	<0.01	<0.001	n.s.

[a]Observed percentage smolt-age-groups among returning adults are significantly less than those at the smolt emigration among 1- and 2-yr smolts, significantly more among 3-yr smolts, and the same among 4-yr smolts.

[b]Calculated from unpublished data kindly provided by W. M. Shearer.

Homing

When adults at sea form a population of mixed origin, maintenance of distinct stock characteristics in individual rivers requires a homing mechanism to ensure segregation to the appropriate river during the spawning migration. Huntsman (1937, 1938, 1939) argued that until individual fish, marked in the river before migrating to sea, were caught at sea beyond the influence of their native river, released again, and finally recaptured in their native river, conclusive evidence of homing was lacking. He later published (1942) such evidence. With the probability of recapture in the Greenland fishery of a tagged British or Irish smolt at about 0.005 (see Swain 1980), and the probability of recapture in home waters of an adult marked in Greenland waters at about 0.0094 (see Jensen 1980b), the chances of satisfying Huntsman's strictures among salmon of the British Isles were of the order of 2×10^{-5}, following the few years when marking was attempted at sea off Greenland. In any case no salmon tagged as smolts were caught at sea by the research vessels, and so the critical evidence of homing to a native river after feeding in the N.W. Atlantic has yet to be obtained.

Harden Jones (1968) proposed that proof of the parent stream theory would be obtained if it were shown that the same differences in characteristics of the smolt populations between rivers were also evident in the adult populations on the spawning grounds of those rivers. He did not specify characteristics in which differences might be found. We have compared age structure of the migrant smolt population of the North Esk River, Scotland, with the smolt-age structure of the adult population returning to the North Esk from that particular smolt migration year, over a period of 15 years (Table 3; data of W. M. Shearer). If smolt age and sea age are independent (Rosen 1918; Dahl 1937; Huitfeldt-Kaas 1946), and the salmon are returning to their native river, then smolt age

structure should be the same at the smolt and adult stages. The significant differences ($P < 0.001$) from this expectation suggests that smolt age and sea age in the North Esk population are not independent. Some river populations have shown an inverse relationship between smolt and sea ages (Esdaile 1911; Alm 1919, 1924, 1934; Hutton 1925, 1937; Menzies 1925; Dannevig 1930; Ritter 1975; Thorpe 1980), and therefore this life history characteristic cannot be used to test the parent stream theory.

However, the discoveries of Cross and Payne (1977), Payne and Cross (1977), and Cross et al. (1978) referred to above, that gene frequencies in two enzyme systems differed in the populations of two neighboring Irish rivers at both the freshwater and adult stages, do provide the conclusive evidence required.

If we relax Huntsman's rigor for a moment, and assume that smolts leaving some British rivers move out of their influence before returning to spawn, data are available (Hawkins et al. 1979) showing that only 2.7% on average stray from 'home.' The accuracy of these data are unknown as the relative levels of exploitation rate in the fisheries from which the recoveries were made are themselves unknown.

To these data should be added those derived from kelt-tagging experiments in Ireland (Went 1969). On 10 Irish river systems, and in the Carrowmore Lake, Co. Mayo, 14 881 spent salmon were tagged. From these, 296 clean fish were recovered, of which 225 were in their native estuary or river, 64 were caught at sea, and 7 were above tidal waters of the "wrong" river. These strays then form 3.0% of all fish recovered in rivers, showing a homing accuracy of 97.0%, similar to that among British smolts.

Larsson (1974) recorded some straying of salmon tagged as smolts in rivers of the west coast of Sweden, with recaptures of adults in Denmark, Germany, and Holland, one even penetrating the Rhine. In studies on the sensory control of orientation in migrating adult salmon in the Baltic, Toft (1975) recorded 7.25% straying among 182 recoveries of control fish, but 58.0, 28.6, and 24.0% straying among 176 neurotomized, 28 partially neurotomized, and 25 blinded fish, respectively.

Experiments reported in Hawkins et al. (1979) revealed recovery in freshwater in the North Esk river of adults tagged as descending migrants in the Girnock Burn, a headwater tributary of the neighboring River Dee, which enters the sea 50 km to the north of the North Esk. It is not known to what extent these fish move out of the North Esk subsequently and enter the Dee. Likewise, Huntsman (1950) recorded many 'foreign' fish in the small Moser River, Nova Scotia, sometimes outnumbering the native stocks. He noted that Moser River fish were caught in the outflow areas of many neighboring rivers, but not in that of St. Mary River, which, although close, drained land of different geological character. His interpretation was that fish avoid unfamiliar water, and that recognition of the appropriate water type may simply stop wandering rather than direct the fish home.

Carlin (1955) postulated that the return migration of salmon occurred in three phases:

1) a directed movement at sea towards the general neighborhood of the river;

2) a wandering to and fro along the coast in that neighborhood; and

3) a rapid migration upriver.

Smith et al. (1981) have recently found evidence of maintenance of a constant swimming direction by maturing adult salmon at sea. Edman (1954) recorded to-and-fro movement of tagged 1-sea-winter salmon, influenced by winds and currents, along the shore of western Sweden, and Hawkins et al. (1979) recorded similar movement from individually tracked adult salmon off the mouth of the North Esk River, Scotland.

For the maintenance of discreteness of stock, it matters more that homing to the native stream occurs than that it is directed from a distance or only locally.

Inherited Differences

Ricker (1972) reviewed the evidence for inheritance to a wide range of characteristics in *Oncorhynchus* spp. The recent development of intensive and extensive salmon culture has encouraged experimental investigations of heritability of traits of commercial importance in salmonids. In *Salmo salar*, systematic studies in Europe began with the development of hatchery production of smolts in Sweden, to compensate for the massive reduction of productive capacity of Swedish rivers when most of these were converted into chains of hydroelectric reservoirs. From tagging experiments Carlin (1965) noted that the total yield from a range of full-sib families released into the Baltic sea varied. Ryman (1970) analyzed the recapture frequencies from some of these releases, and demonstrated genetic components of variance. He also established (Ryman 1972a) genetic components of variance in the weights of these fish at recapture. Thus survival and growth performance at sea were shown to be influenced by parental type.

Mortality of juvenile salmon during the period just prior to their release into the Baltic was studied among 37 families in seven groups of various geographic origin, by Ryman (1972b). Environmental and genetic components of variance were separable, and he showed that although environmental influences were very strong, there were significant differences between families within groups, and between groups. However, there were no clear distinctions between mortality responses from separate river stocks. Kanis et al. (1976) also showed that mortality at the egg and alevin stages among Norwegian salmon was heritable.

Lindroth (1972) in Sweden, and Naevdal et al. (1975) in Norway, found high values of heritability for weight and length, respectively, of juvenile salmon. Their analyses were not strictly valid, as normality of distribution of weight and length among sibling populations is uncharacteristic at that stage. It has been shown (Simpson and Thorpe 1976; Thorpe 1977; Thorpe and Morgan 1978, 1980; Bailey et al. 1980) that these variables are distributed bimodally, and therefore comparisons should be made between the means of comparable modal groups and between the proportions of numbers in these groups. Thorpe (1977) made such comparisons between replicated underyearling populations derived from wild salmon parents from the River Almond, Scotland, and showed significant differences in length and in proportions in the upper modal group (percentage 1-yr smolts) attributable to parentage. Subsequent experiments with half-sib populations (Thorpe and Morgan 1978) showed that sire and dam com-

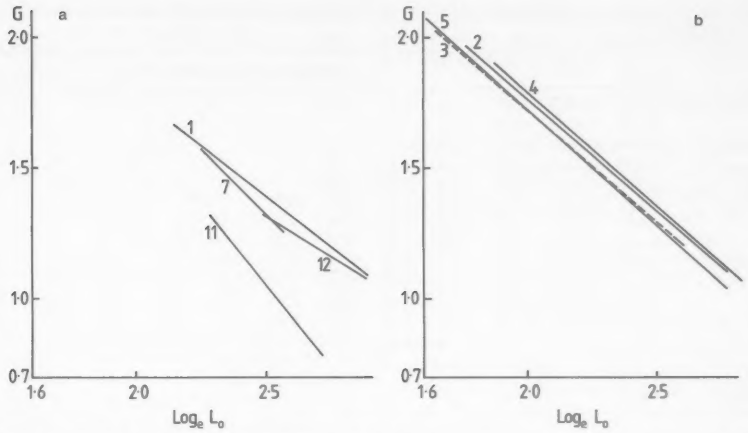

FIG. 5. (a) Regression of specific growth rate during the 1st year at sea, on logarithm of mean length at the formation of the last freshwater annulus, for four northwest Scottish rivers. (b) Comparable regressions for four neighboring Scottish east coast rivers.

ponents of variance in growth and in developmental rate (percentage 1-yr smolts) differed. An indication of a paternal influence over developmental rate was reinforced when individual females were paired with a series of males of differing ages from mature parr to 2-sea-winter fish, and the progeny of the parr were shown consistently to produce the highest proportions of 1-yr smolts, irrespective of female characteristics (Thorpe and Morgan 1980). Maternal influences on size of progeny were evident in all these experiments also. Refstie and Steine (1978) compared mean lengths and weights in their first autumn of 308 families of juvenile salmon, derived from 32 "strains" in Norway over 3 years. Thirteen of these strains were from salmon caught at sea and therefore of unknown river origin: most of the others were derived from fish caught in rivers, but a few were from farm stock. No account was taken of bimodality of size distribution within these populations, so unfortunately the mean lengths and weights and the analyses are invalid. This might account for the wide ranges of variation evident: -0.7 to $+0.85$ SD units about the overall mean for all rivers, with the River Vosso sample showing from -0.7 to $+0.65$.

Refstie and Kittelsen (1976) found differences in percentage 1-yr smolts among progeny of salmon from the River Vikja and of salmon caught in the sea at Måløy, Norway. These young fish were reared under the same conditions at the Sunndalsøra experimental station. Later, Refstie et al. (1977) showed differences in percentage 1-yr-smolt production among families derived from 37 Norwegian localities over 4 years, and also reared at Sunndalsøra. While establishing undoubted genetic influences over smolting rate in these Norwegian salmon, and indicating possible distinctions between river stocks in this trait, the authors noted that material from any one river was limited and large-scale testing would be needed to establish real genetic differences between the stocks as a whole.

Gunnes and Gjedrem (1978) reported on trials in which representatives of the 37 Norwegian strains were grown in five sea-cage sites for 2 years. Three year-classes of progeny were used. The fish were weighed and measured at slaughter, and although there were significant differences in size attributable to differences in the farm sites, differences due to strains were predominant. Heritabilities, estimated from sire components, for weight and length were high at 0.31 and 0.28, respectively. Again, this is evidence for genetic distinction in growth capacity between separate river stocks, but as with the findings of Refstie et al. (1977), requires confirmation with more extensive material.

Although data suitable for comparing river stocks reared under similar environmental conditions are not available from the British Isles, an alternative comparative approach is possible. It was shown above that on entry to the sea, smolts from different river populations intermingle on feeding grounds. It is therefore reasonable to consider that smolt populations from local groups of rivers grow during their 1st year at sea under similar environmental conditions. As length at age differs within the freshwater phase of growth in different river populations, comparison of growth performance during the 1st sea year is best made between measures of proportionate increases in length rather than between absolute lengths at the end of that year. Such data are available for most of the 74 rivers referred to earlier.

The linear regression of specific growth rate G, on $\log_e L_0$, the mean length at the end of the last river year, where:

$$G = \frac{\text{Log}_e L_1 - \text{Log}_e L_0}{t_1 - t_0}$$

where L_1 is mean length at t_1, L_0 is mean length at t_0, t_1 is the end of the 1st sea year, and t_0 is the end of the last river year, was calculated for each river from scale-reading data in the literature. The regressions for four northwest Scottish rivers (Fig. 5a) illustrate differences between populations. Regression coefficients for 12 Scottish rivers have been compared (Tables 4 and 5), and show that growth performances

TABLE 4. Significance of differences between slopes of the regressions of specific growth rate in length during the 1st year at sea, on length at the last winter in freshwater.[a]

River	*b*-value	±SE	*t*-value for difference between pairs											
1. Morsgail	−0.769	0.1125												
2. Tay	−0.858	0.0257	0.77											
3. Dee (Aberdeen)	−0.866	0.0163	0.85	0.26										
4. North Esk	−0.870	0.0246	0.88	0.34	0.14									
5. Spey	−0.884	0.0266	1.00	0.70	0.58	0.39								
6. Nith	−0.910	0.0392	1.19	1.11	1.04	0.86	0.55							
7. Hope	−0.984	0.1391	1.20	0.89	0.80	0.81	0.71	0.51						
8. Tweed	−0.949	0.0146	1.59	3.08	3.86	2.76	2.15	0.93	0.25					
9. Dee (Kirkcudbright)	−0.993	0.0320	1.94	3.29	3.53	3.04	2.62	1.64	0.06	1.25				
10. Conon	−0.996	0.0375	1.92	3.03	3.18	2.81	2.44	1.58	0.08	1.17	0.06			
11. Grimersta	−1.247	0.0357	4.06	8.83	9.70	8.68	8.15	6.35	1.83	7.70	5.29	4.84		
12. Ewe	−0.605	0.0434	1.36	5.02	5.63	5.31	5.48	5.21	2.60	7.51	7.19	6.82	11.42	
			1	2	3	4	5	6	7	8	9	10	11	12

[a](—) $P < 0.01$; (- - -) $P < 0.05$.

TABLE 5. Significance of differences between positions of the regressions of specific growth rate in length during the 1st year at sea, on length at the last winter in freshwater.[a]

River	*a*-value	SE	*t*-value, for difference between pairs											
			1	2	3	4	5	6	7	8	9	10	11	12
1. Morsgail	1.329	0.0236												
2. Tay	1.577	0.0077	10.00											
3. Dee (Aberdeenshire)	1.455	0.0043	5.26	13.90										
4. North Esk	1.477	0.0050	6.14	10.94	3.33									
5. Spey	1.369	0.0060	1.64	21.43	11.68	13.86								
6. Nith	1.394	0.0122	2.45	12.69	4.70	6.28	1.84							
7. Hope	1.402	0.0181	2.45	8.89	2.84	3.99	1.73	0.37						
8. Dee (Kirkcudbright)	1.374	0.0109	1.73	15.31	6.95	8.64	0.40	1.22	1.33					
9. Tweed	1.446	0.0013	4.95	53.46	2.01	6.02	12.62	4.23	2.42	6.61				
10. Conon	1.334	0.0062	0.21	24.67	16.02	17.94	4.06	4.30	3.55	3.21	17.70			
11. Grimersta	1.079	0.0044	10.41	56.22	60.57	59.34	3.91	24.19	17.29	25.19	79.13	33.35		
12. Ewe	1.234	0.0049	3.94	37.73	33.82	34.66	17.45	12.14	8.94	11.78	41.84	12.63	23.34	

[a](—) $P < 0.01$; (- - -) $P < 0.05$.

of populations from neighboring rivers differ significantly during this 1st year at sea.

This analysis shows that whereas the deceleration of growth during the 1st year at sea is similar between river populations over broad geographical areas in Scotland, the actual growth rate achieved by individual fishes of a specific size differs between river populations (Fig 5b). This is particularly clear from data on the major salmon-producing rivers of the Scottish east coast, the Tay, Dee, North Esk, and Spey. Their rates of decrease of specific growth rate with fish size were the same (Table 4) (but differed from those of populations from many rivers elsewhere in Scotland): but the mean value for specific growth rate for fish of any given size differs between the four rivers (Table 5). The neighboring southwest rivers Nith and Dee (Kirkcudbright), however, show differences in neither slope nor position of the regressions, so that their populations exhibit the same growth capacities at sea.

Such an analysis cannot fully distinguish genetically and environmentally induced differences. Local coastal environmental differences at first entry to the sea, and slight differences in routes by which the component populations reach common oceanic feeding rounds, may influence these specific growth rate relationships. However, the existence of real differences in these mathematical relationships, based on measurements made on returning adults, reinforces the conclusion that the separate rivers harbor distinct salmon stocks.

Heritability of maturation rate in Atlantic salmon has been a source of speculation for many years, and is assumed in the theoretical treatment of life history evolution among salmon by Schaffer (1979) and Schaffer and Elson (1975). Thorpe (1975) showed that the proportionate occurrence of mature parr among the males in sibling populations differed between families. Thorpe and Morgan (unpublished data) have recently found that such mature parr show among their progeny higher proportions of mature parr than do older sea-run males. Piggins (1979) conducted a series of experiments over 6 years to test the hypothesis that grilse (1-sea-winter salmon), breed grilse, and 2-sea-winter salmon breed 2-sea-winter salmon

TABLE 6. Sea winters before first maturity of progeny of parents of various sea-winter types, reared and released at Newport, Co. Mayo, Ireland. (Data from Piggins 1979.)

Parent-type sea winters	Progeny-type sea winters					
	0		1		2	
	No.	%	No.	%	No.	%
1×1	5[a]	0.2	3227	98.1	55	1.7
1×2	—	—	147	96.1	6	3.9
2×2	—	—	183	87.1	27	12.9

[a]Pregrilse: i.e. returning to freshwater before spending a winter at sea.

(Table 6). It was evident from these data that sea absence was influenced genetically, but that environmental influences on maturation rate dominated in this area off western Ireland. Simpson and Thorpe (1976) postulated that age at first maturation was determined in a population by the inheritance of specific levels of sensitivity to environmental cues, at which the physiological decision to mature sexually is taken. Schaffer and Elson's (1975) hypothesis that reproductive age of a salmon stock is selected in relation to the optimal allocation of energy to reproduction is in accordance with their assumption of discrete breeding stocks in each river and the observed differences in age structure of returning adult populations. Martin and Mitchell (unpublished data) have shown that the age structures of a single river stock and of regional Scottish stocks have changed in relation to sea temperatures in the North Atlantic over a 25-yr interval. Within this interval high proportions of grilse have been associated with high mean weights of these fish. Year-to-year variation in age structure of supposedly discrete stocks implies that comparisons of population age structures as indications of differences between river stocks are valid only if made over comparable intervals of years.

Conclusions

Menzies' (1939) definition of a stock depended on the reproductive isolation of that population unit from other units. The unequivocal demonstration of such isolation depends on the comparison of population characteristics determined entirely genetically, and on which environment can have had no influence. Of all the evidence for discreteness of Atlantic salmon stocks in the British Isles which we have reviewed above, only one case, that of the populations of the Rivers Bandon and Blackwater, can be considered unequivocal. However, the mechanisms enabling the maintenance of such reproductive isolation, namely segregation from the mixed feeding population at sea, and high precision of homing to the native river, are evident from a much wider geographical range. The heritability of physiological capacities, such as growth and maturation rates, has been shown under controlled hatchery environments, and at least with specific growth rate at sea it is evident that different river populations show differences in performance. Thus, although these and morphological differences are not of themselves sufficient evidence for the distinct nature of river stocks, they are strong circumstantial evidence in support of such a hypothesis. It is reasonable to predict that when data are available on the allele frequencies of ranges of polymorphic protein systems for river populations of salmon throughout the British Isles, these data will confirm that hypothesis.

Implications for Management

To what extent are these conditions incorporated in present management practices? In considering management, the working group on North Atlantic salmon of the International Council for the Exploration of the Sea concluded (Anon. 1979) that:

1) maintenance of optimal spawning escapement was made more difficult as the ratio of river exploitation: mixed stock exploitation decreased;

2) stocks from less-productive rivers may be seriously depleted or eliminated if exploited together with other more productive river stocks in a large mixed fishery;

3) non-catch fishing mortality was higher on feeding grounds than when mature salmon were caught approaching their home rivers;

4) sea fisheries remote from rivers of origin reduced salmon biomass returning to them;

5) mixed-stock fisheries reduced the accuracy with which catch statistics could be obtained for individual river stocks; and

6) exploitation of salmon during a period when they were growing rapidly was likely to reduce the yield per recruit.

The logical step should then be to restrict exploitation to the stages after which individual stocks have segregated.

The national and international salmon-fishery regulations existing in 1980 go some way, but only part way towards achieving the goals of optimal spawning escapement, protection of individual stocks, avoiding wastage through non-catch fishing mortality, maintenance of maximum biomass, procurement of accurate stock statistics, and maintenance of optimal yield. In the United Kingdom and Ireland protective regulation varies regionally.

IRELAND

Ninety-eight percent of the Irish fishery is commercial, as opposed to recreational. Seventy-five to eighty percent of the catch since 1974 has been by drift net at sea, where netting is licensed from March 16 to July 20, within the 12-mile limit. As noted above, fish originating in many distant rivers have been taken in this fishery, and data from Irish tagging experiments have shown that for every smolt recovered in the home river as an adult, 4.5 more have been taken in the drift-net fishery (Piggins 1980). Since 1975 the catch has declined, and the escapement into the Shannon and Burrishoole rivers in 1978 was estimated at 33 and 50%, respectively, of the 10-yr mean. There is now doubt about the adequacy of recent escapement to ensure future recruitment.

ENGLAND AND WALES

Salmon fishing is licensed within 6 miles of the shore, and flexibility exists to apply additional restrictions to conserve specific river stocks. In the early 1960s, 25% of the catch was taken by coastal and drift nets off the northeast of England: by the late 1960s this had increased to 50%. Recent experiments tagging adult fish taken in the drift-net fishery have shown

that most of these fish were en route to Scottish rivers.

SCOTLAND

Between 1960 and 1978, 43% by number of the Scottish salmon catch was taken commercially by nets fixed to the shore outside estuarial limits, and the remaining 57% by seine nets within estuaries and the lower reaches of rivers, or by angling (Anon. 1962–80). There is an annual close season of 168 d, and a weekly close time of 42 h. Drift-netting is prohibited. Repeated tagging experiments with fish caught in bag nets at coastal sites (Calderwood 1923; Menzies 1937, 1938a, b; Pyefinch and Woodward 1955; Pyefinch and Shearer 1957; Shearer 1957) have shown wide dispersal of such fish along the coasts, such that some net stations, especially in the north and northwest, catch fish destined for rivers up to 660 km distant. (Similar wide dispersal was shown by fish caught and released from coastal nets on the north, west, and south coasts of Ireland (Gibson 1953; Went 1951, 1953; Went and Gibson 1953; Went and Vickers 1953, 1956).) Consequently these nets at open coastal sites are often fishing mixed stocks, and only nets within river mouths can be considered likely to concentrate on a distinct stock.

In 1965 the Hunter Committee, a government body appointed to review the law relating to salmon and trout fisheries in Scotland, recommended (Anon. 1965) among other things that: "If Scottish salmon fisheries are to be used to produce the maximum benefits for the country, the methods of controlling the fisheries must be capable of something more positive than maintaining the spawning stock, vital though that is. The existing methods of regulation . . . must be replaced by a system of management under which the right numbers of fish are caught in the ways that bring the greatest advantage. . . It should ensure that the breeding escapement is sufficient without being excessive. It should provide a way of measuring as accurately as possible the effect of any changes which have occurred naturally or by design . . . These considerations have convinced us that some fresh approach to management is needed which recognises and takes full advantage of the basic fact of homing . . . we believe that commercial fishing should be permitted only in the river . . . as a salmon taken in the sea cannot with certainty be identified with its native stream . . . The full implementation of the management policy . . . would require that salmon fishing in the sea should be prohibited. This would entail the running down of all coastal netting, and its eventual replacement by new methods of fishing . . . whereby the commercial catch from the river is taken at only one point." This single point fishery was seen as a trap or a concentration of nets.

The use of drift nets and other gill nets to catch salmon at sea is now prohibited, but some coastal trap nets still exploit mixed stocks of salmon.

Acknowledgments

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Applications of the Stock Concept to Fish Populations in the USSR[1]

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ALTUKHOV, YU. P., AND E. A. SALMENKOVA. 1981. Applications of the stock concept to fish populations in the USSR. Can. J. Fish. Aquat. Sci. 38: 1591–1600.

Genetic studies of several species of marine fish conducted for over 20 years are reviewed for their application to the problem of intraspecific differentiation of fish. Cytophysiological, biochemical, and immunological methods were used. By each of these, two sizes of Black Sea horse mackerel (*Trachurus mediterraneus*) were shown to be sibling species and not local stocks. Similarly, North Atlantic redfish *Sebastes marinus* and *S. mentella* were found to be separate species, in agreement with known morphological and ecological differences. In Pacific salmon, genetic markers were used to distinguish planted chums from native stocks, and indicated that such populations are maximally adapted to their historic environment. Stock differences are less apparent in pinks, but are sufficient to suggest subpopulation structure. Genetic differences are found in adjacent generations in odd and even years. Subdivision was most pronounced in sockeye salmon (*Oncorhynchus nerka*). Spring sockeye spawning in streams were more subject to selection pressure than were summer stocks spawning in lakes. In Atlantic salmon (*Salmo salar*), spawning in rivers of northern European USSR, the majority showed genetic subdivision during the spawning run. North Sea herring (*Clupea harengus*) tested by hemagglutination reactions showed differences that coincided with ecological subdivision at spawning, for winter–spring oceanic, summer–autumn marine, and spring–summer coastal herring. Electrophoretic determinations supported these differences. In European anchovies (*Engraulis encrasicholus*), stocks were differentiated by blood groups, even in the absence of spatial isolation. All of these findings indicate that elementary fish populations play an important role in differentiation and integration of the species gene pool. Efficient management of fish stocks is based on preserving the hereditary heterogeneity of their populations.

Key words: genetic markers, stock differences, immunological, biochemical, physiological, intraspecific differentiation

ALTUKHOV, YU. P., AND E. A. SALMENKOVA. 1981. Applications of the stock concept to fish populations in the USSR. Can. J. Fish. Aquat. Sci. 38: 1591–1600.

Les auteurs font le point sur les études génétiques de plusieurs espèces de poissons de mer menées en ces 20 dernières années et sur leur application aux problèmes de différenciation intraspécifique chez les poissons. Ils ont utilisé des methodes cytophysiologiques, biochimiques et immunologiques. Grâce à ces méthodes, ils ont démontré que deux groupes de taille de saurels (*Trachurus mediterraneus*) sont des espèces jumelles et non des stocks locaux. De même, on a trouvé que, en accord avec des différences morphologiques et écologiques connues, les sébastes de l'Atlantique nord, *Sebastes marinus* et *S. mentella*, sont deux espèces distinctes. Chez les saumons du Pacifique, on a utilisé des marqueurs génétiques pour séparer saumons keta ensemencés et stocks indigènes; ces marqueurs ont en outre indiqué que de telles populations étaient adaptées au maximum à leur environnement historique. Les différences entre stocks sont moins apparentes chez les saumons roses, mais quand même suffisantes pour suggérer des sous-populations. On observe des différences génétiques entre années impaires et paires dans des générations adjacentes. Ces différences sont plus prononcées chez les saumons nerka (*Oncorhynchus nerka*). Les saumons nerka de printemps frayant dans les cours d'eau sont plus sujets à la pression de la sélection que les stocks d'été frayant dans les lacs. Chez le saumon atlantique (*Salmo salar*) frayant dans les rivières du nord de l'URSS européenne, il apparaît dans la majorité une subdivision génétique au moment de la remontée de ponte. Des réactions d'hémaglutination ont démontré chez le hareng (*Clupea*

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harengus) de la mer du Nord des différences coïncidant avec une subdivision écologique lors de la ponte, pour les harengs océaniques frayant en hiver–printemps, les harengs de mer frayant en été–automne et les harengs côtiers frayant au printemps–été. Des déterminations électrophorétiques confirment ces différences. Chez l'anchois européenne (*Engraulis encrasicholus*), les stocks peuvent être différenciés par groupes sanguins, même en l'absence d'isolation spatiale. Toutes ces observations indiquent que les populations simples de poissons jouent un rôle important dans la différenciation et l'intégration de l'effectif des gènes de l'espèce. Une gestion efficace des stocks de poissons est fondée sur la préservation de l'hétérogénéité héréditaire de leurs populations.

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THE genetic trend in marine biology, aimed at studying intraspecific differentiation of fish on the basis of immunological, biochemical, and physiological characters, began about 20 years ago. The characteristics of the immunological approach have been examined in a number of publications (Marr and Sprague 1963; Cushing 1964; Altukhov et al. 1964; Altukhov 1969; Suzuki 1967; de Ligny 1969).

During this period the biochemical genetics of fish populations was developed intensively. Reviews of these investigations, and of the general achievements, prospects, and applied effects in this field have been made by many authors (Møller 1968, 1970; de Ligny 1969, 1972; Altukhov 1973, 1974, 1977; Utter et al. 1974; Allendorf and Utter 1978, Kirpichnikov 1979).

In the work of Soviet authors in the field of cell physiology of poikilothermic animals, a new feature, thermostability of isolated cells (Ushakov 1959a, b), has been shown to be convenient for distinguishing taxonomically closely related species (within one genus) and, in certain cases, also for intraspecific groups. Some biochemical and immunological data (V. B. Ushakov 1963, 1965; Altukhov 1965a, b) show that the heat killing of isolated cells, indicated by the irreversible loss of electrical excitability, is due to denaturation of soluble sarcoplasmic proteins. Recently the polygenic nature and heritability (h^2) of thermally induced cell death were established (Altukhov et al. 1967a; Altukhov and Ratkin 1968; Ushakov et al. 1967). Details of this cytophysiological trend in research connected with speciation are discussed by Ushakov (1959a, 1964, 1967).

This report sums up the main results of 20 years of Soviet genetic studies of intraspecific differentiation of marine fishes, such as Black Sea horse mackerel *Trachurus mediterraneus*, Black and Azov Sea anchovy *Engraulis encrasicholus*, *marinus* and *mentella* redfish from the North Atlantic, the North Atlantic herring (*Clupea harengus harengus*) and Pacific herring (*C. harengus pallasi*), Atlantic salmon (*Salmo salar*), and Pacific salmon (*Oncorhynchus* spp.).

Studies on the Differentiation of "Large" and "Small" Forms of the Black Sea Horse Mackerel

In the 1940s, numerous large horse mackerel (50 cm and more) were discovered in the Black Sea. They were biologically different from the small mackerel (less than 20 cm) commonly found there. In particular, the "small" form matures in its 2nd year and spawns in coastal waters, the "large" fish matures at 4 yr of age and spawns in the open sea.

However, because of the absence of external morphological differences, both types were considered to be the same species, *T. mediterraneus* (Numann 1956; Aleev 1956, 1957, 1959). Aleev maintains that "large" horse mackerel may be considered an independent southern (Anatolian) "local stock" differing biologically from the "local stocks" of the northern (Crimean) and eastern (Caucasian) "small" forms. No definite data have been cited on "large" horse mackerel existing outside of the Black Sea.

Cytophysiological, immunological, and biochemical investigations of the Black Sea horse mackerel gave the following results.

1) "Small" horse mackerel of both the northern and eastern "local stocks" do not differ in respect to thermostability of isolated muscle tissue, whereas the "large" type (around 40 cm long) differs sharply from both small stocks in this respect. When seasonal changes of this feature are taken into account (Altukhov 1963), the cell thermostability[2] (CT) of "large" and "small" horse mackerel differs by 2°C on the test temperature scale, i.e. it appears to be similar to that between taxonomically close species (Altukhov 1962a, 1967a; Altukhov and Glushankova 1966; see also Kusakina 1959, 1960; Ushakov 1964, 1967). The above difference is due to genotypical adaptation at the cellular level. A higher CT is characteristic of the more heat-loving "large" mackerel.

2) The CT analysis of several hundred horse mackerel, less than 20 cm long, established the heterogeneity of samples taken from populations inhabiting Black Sea coastal waters. The distribution of CT is bimodal, the mean value of the right-hand side of the frequency curve being identical with the cell thermostability level peculiar to "large" fish. This fact, indicating young "large" horse mackerel live in mixed populations with "small" fish, was used to elucidate peculiarities of winter distribution of young of the "large" form off the Caucasian and Crimean coasts (Altukhov and Glushakova 1963). It likewise allowed us to measure the difference in thermostability of actomyosin proteins of these forms (Glushankova 1963), as well as permitting comparisons of otoliths, which also differed (Altukhov and Mikhalev 1964).

3) The cytophysiological difference between the "large" and "small" horse mackerel was also shown by serological tests. Precipitin titers of muscle extracts showed that Black

[2]"Cell thermostability" is synonymous with "muscular thermostability," as muscle heat death is indicated by irreversible loss of excitation of separate fibers most resistant to heat. For brevity we term this property "CT," the preparation survival time at different temperatures.

Sea horse mackerel differ from each other no less than from the mackerel *T. trachurus*, which is known to be a distinct species (Altukhov and Apekin 1963). Later, when the CT of *T. trachurus* was studied in the North Sea, and the data obtained compared with the results for the Black Sea horse mackerel, we found the same picture (Altukhov 1967b).

4) Differences within the Black Sea horse mackerel were likewise found when studying the antigenic properties of their erythrocytes (Limansky 1965) and serum heteroagglutinins (Limansky 1967). When human erythrocytes were agglutinated with horse mackerel sera, the "large" forms proved to differ sharply in this respect from nearly all the mutually identical "small" forms from local stocks.

However, paper electrophoresis tests of serum proteins indicated only a slight difference between "large" and "small" horse mackerel in the α-globulin zone (Golovko 1964). Considering the low resolution of the above method, as well as data on the character of protein difference in sibling species (Hubby and Throckmorton 1968), one may expect to find a more significant differentiation of horse mackerel in future by electrophoretic analyses of their proteins, particularly myogens and hemoglobins.

5) The sum of the results reviewed above, indicating a strong divergence of "large" and "small" mackerel in a whole series of genetic features (both polygenic and mendelian) does not permit us to consider these forms merely as "local stocks." Bearing in mind the striking outer similarity of these forms, they should be given the status of sibling species, one of which, the "large," is in all probability a migrant from the Mediterranean (Altukhov 1962a, b). This viewpoint is supported by the report that "large" horse mackerel are known to exist beyond the Black Sea (Slastenenko 1965).

Studies on the Differentiation of the North Atlantic Redfish *marinus* and *mentella*

Cytological, immunological, and biochemical studies were conducted to elucidate the difference between the redfish (*Sebastes marinus*) and deepwater redfish (*S. mentella*), there being differing opinions regarding their taxonomy (Travin 1951; Andrijashev 1954; Kotthaus 1961).

1) The CT of over 1000 redfish caught in the waters off Iceland, Greenland, Labrador, and in the Barents Sea was studied from 1964 to 1966 aboard research vessels. In this respect *marinus* and *mentella* differ no less than independent species do, the *mentella* cells being more resistant to the lethal effect of heat. This result was obtained with fish samples both in the Northwestern (Altukhov et al. 1967*a*) and northeastern Atlantic (Payusova and Nefyodov 1968). Taking the correlation of the CT level to habitat temperature as the rule established for more than 300 poikilotherm species (see Ushakov 1964, 1967), one may infer that *mentella* are more thermophilic.

2) CT analysis for those redfish which, because of their external morphology, occupy an intermediate position between *marinus* and *mentella*, reveals a bimodal distribution. Moreover, the CT of the "intermediate" redfish (22.75 ± 0.75 min at 28°C) likewise proves to be "intermediate" at the same test temperature for *marinus* (13.6 ± 0.69 min) and *mentella* (27.8 ± 0.69 min) in the Iceland area.

It is essential to stress that the West Greenland *marinus* redfish has a CT (20.05 ± 0.58 min) very close to that of the "intermediate" redfish. However, the distribution curve of their CT values has only a single peak. This fact, considered with the biological data (Zakharov 1962) on the juvenile nature of the females belonging to the West Greenland *marinus* population, leads us to assume a hybrid (F_1) origin for such fish. The absence of maturation in West Greenland *marinus* females, as well as in "giant" redfish females frequently encountered there, has been proved immunologically: their ovovitellin synthesis is suppressed (Altukhov et al. 1967*b*).

3) Agar-gel electrophoresis of blood serum proteins from *marinus*, *mentella*, and "giants" showed frequency differences in some protein components (Altukhov and Nefyodov 1967). Polymorphism, probably hereditary and two-allelic, has been noted in the redfish albumin zone. At the same time, the low concentration of "slow" albumin in the blood of assumed heterozygotes, and the small number of samples give no ground for considering the previous conclusion as final. The hereditary variability of electrophoretic mobility in the redfish serum proteins seems more certain for some haptoglobin types, the frequencies of which helped reveal the distinctions between *marinus* and *mentella* (Nefyodov 1969).

On the whole, our biochemical data are in agreement with the results of previous investigations by O'Rourke (1961) and Schaeffer (1961), who determined the difference in *marinus* and *mentella* by the antigenic properties of blood serum and the protein amino acid composition of gill mucus and muscles. The new information deals with the "giant" redfish. Notwithstanding its strong outward similarity to *marinus*, there is no biochemical identity between the two forms (Altukhov and Nefyodov 1967). This fact is in accordance with the assumption of the hybrid origin of the "giants" (see 2). Recently Naevdal (1978) has found that *mentella* and *marinus* differ in electrophoretic patterns of hemoglobins and discovered in some redfish hemoglobin of "hybrid" type.

4) Thus, the cytophysiological, biochemical, and immunological data indicate a clear divergence between *marinus* and *mentella* redfish. This is also in sound agreement with the generally known morphological and ecological peculiarities of the two forms which may obviously be considered separate species.

Population–Genetic Studies of Pacific and Atlantic Salmon

Population–genetic studies of salmon are of particular theoretical and practical value in view of the following circumstances: (1) salmonid species have been extensively studied, both biologically and ecologically; (2) a strong homing characteristic of most salmonid species permits the development of intraspecific divergence in accordance with the geographical characteristics of spawning regions; (3) several salmonid species have been artificially propagated for many years.

Studies have been carried out since 1968 by the Institute of Marine Biology of the Far-Eastern Research Centre and the Institute of General Genetics, of the USSR Academy of Sciences on chum salmon (*Oncorhynchus keta*) pink salmon (*O. gorbuscha*), and sockeye salmon (*O. nerka*) of Sakhalin, the Kuril Islands, Kamchatka, and the Amur River. Chum salmon are represented mainly by artificially reproduced

spawning populations from several hatcheries in Sakhalin, the Kuriles, and on the Amur River; pink salmon — both by natural and artificially maintained spawning populations from the same regions; sockeye salmon — by the naturally spawning isolated stock inhabiting Lake Azabach in the Kamchatka River basin.

The methodological approach includes (1) detection and investigation of hereditary protein polymorphism by different electrophoretic methods in these species; (2) a detailed study of the distribution of corresponding genotypes (phenotypes) and genes in space and time; (3) the use of the genetic data for analysis of the results of the work of hatcheries, and some stock transfers.

1) In chum salmon the following polymorphic protein systems were studied: lactate dehydrogenase (LDH), malate dehydrogenase (MDH), blood serum albumin-like lipid-containing protein (ALB, conditionally), isocitrate dehydrogenase (s-IDH), and aspartate amino-transferase (AAT). Inheritance of a number of systems was tested in special breeding studies with chum and other salmon species (Sachko 1973; Altukhov 1974; Allendorf et al. 1975; May et al. 1975).

Analysis of chum samples made periodically during a spawning run reveals in many cases significant intrapopulation heterogeneity for phenotypic or gene frequencies. This is mainly true of the allele frequencies at the LDH-B^2 and ALB loci, and to a lesser degree in the MDH phenotype frequencies. The intrapopulation heterogeneity is, as a rule, more significant in years of high chum salmon abundance. Such genetic heterogeneity apparently reflects the subdivision of a stock into several genetically different subpopulations, analogous to the genetic subdivision discovered previously in the Azov anchovy and the North Atlantic redfish (Altukhov 1969; Altukhov et al. 1969a, b).

Analysis of gene frequencies in space reveals differentiation among separate stocks having different degrees of variability at different loci. The clearest differences are observed between populations spawning on the southwestern and eastern coasts of Sakhalin. The differences are most pronounced for gene frequencies of the MDH, s-IDH, LDH-A^2 loci and less pronounced for other genes. The differences in gene frequency at the LDH-A^2 locus are most significant between the Sakhalin, Kuril and Amur River populations; the Naiba River population is distinguished from practically all other populations studied, including Japanese and American ones (Numachi et al. 1972; Utter et al. 1973) by a substantial frequency of the heterozygous phenotype at the MDH-B locus. In the Teplov population the MDH and LDH-A^2 loci are practically monomorphic. Thus, almost every one of the populations studied has its own genetic peculiarities distinguishing it from the other populations, the characteristic frequencies of most genes remaining stable from year to year.

The distinctive genetic features of stocks make it possible to discover any admixture of transplanted fish in the stock under study after transfer of artificially fertilized eggs. A detailed study of the results of such transfers both within Sakhalin and from Sakhalin to the Amur River has revealed their inefficiency. For instance, the return for the Kalininka River chum salmon (West coast of Sakhalin) transferred as eggs to the Naiba River (East coast of Sakhalin) proved to be 5–10 times lower than the return to the native river. Analysis of the Teplov population of chum (Amur River basin), into which about 200 million eggs at one time were transferred from Sakhalin, has revealed no mixture of Sakhalin chum in the Amur River, which proves the complete failure of this transplant attempt. After transfer of Kuril chum eggs to Sakhalin, their presence was indicated by their genetic markers in the first return, but the future fate of this transfer is still unknown. In this case also, the magnitude of return to a "foreign" river was significantly lower than the return to the "native" river. All these data permit us to regard chum salmon stocks as highly independent populations maximally adapted to their historical environments. Negative results of many egg transplantations suggest the unique and conservative character of this adaptation (Altukhov 1974; Altukhov et al. 1981; Ricker 1972).

2) The population–genetic structure of pink salmon has some differences from the structure of chum salmon. To study it we used the following polymorphic enzyme systems: malate dehydrogenase (MDH-A and MDH-B), α-glycerophosphate dehydrogenase (AGP), phosphoglucomutase (PGM), 6-phosphogluconate dehydrogenase (6PGD), and isocitrate dehydrogenase (s-IDH). Inheritance and genetic control of these polymorphic systems in pink salmon have been studied by Aspinwall (1973a, b) and by Altukhov et al. (1981).

Interpopulation differences among pink salmon within the Sakhalin–Kuril region are less manifest than in chum. The populations spawning on the west coast are quite similar to the populations inhabiting the east coast waters of Sakhalin. Small but statistically significant differences were found for the MDH-A and AGP-S gene frequencies between the total Sakhalin and Kuril samples taken in 1979 as well as between the total Sakhalin and the Amur River samples of 1975. In some year-classes, statistically significant differences were observed in allele frequencies at several loci, between some stocks of the southeast Sakhalin rivers. The range of interpopulation variation of gene frequencies for nearly all the loci is of the same order of magnitude (except for the s-IDH locus, for which the polymorphism is not yet genetically interpreted, and the variation of phenotypic frequencies is expressed to a larger extent).

More significant genetic distinctions are observed between the American and Asian complexes of populations for the MDH-B and especially AGP gene frequencies when comparing our data (Salmenkova et al. 1979) with those of Aspinwall (1974).

Intrapopulation genetic heterogeneity (i.e. heterogeneity between samples taken periodically from a population entering a river for spawning) is not always detected, and not at all loci. The highest variability during a spawning run is characteristic of the s-IDH phenotype frequencies, the 6PGD genotype and gene frequencies, and to a lesser degree of the PGM and MDH-A gene frequencies. On the whole, intrapopulation heterogeneity in pink salmon is expressed to a higher degree than is interpopulation heterogeneity. As in the case of chum, it suggests the existence of a subpopulation structure, but which is less developed in pinks. One of the causes may be a greater mixing, both among individual spawning sites and among populations of individual rivers, associated with a less-developed homing (Aspinwall 1974) and widely used transfers of fertilized eggs (within the Sakhalin–Kuril region). It can also be suggested that a certain contribution to

such a genetic structure is made by constant selective forces which maintain gene frequencies at rather high levels and which differ in the Asian and American populations. This integrating pressure is opposed by genetic drift resulting from sharp fluctuations of pink population size and probably by a fluctuating selective pressure occurring as a result of environmental changes. Apparently, the effects of genetic drift are more pronounced at the subpopulation level, and it is probable that drift is responsible for intrapopulation heterogeneity.

The most interesting feature of pink salmon population structure is shown by genetic differences between adjacent generations reproducing in odd and even years. Pink salmon are known to spawn and die in their 2nd year of life, so they exist as two nonoverlapping (or overlapping slightly as a result of a negligible mixture of other ages) generations in odd and even years. Genetic differences were first noted by Aspinwall (1974), who studied the pink generations of 1969 and 1970 for the frequencies of the MDH-A, MDH-B phenotypes, and AGP genes. Our data obtained from the study of pinks in 1974–79 also reveal population–genetic differences between generations (Salmenkova et al. 1979). Differences in phenotype and gene frequencies are observed for all the loci studied; they are of similar magnitude in all the populations studied in all pairs of generations, and are comparable in the American and Asian populations. Thus, the PGM locus is practically monomorphous in even years, but polymorphous in odd years; in even years the frequencies of the MDH-A and MDH-B common phenotypes increase and the frequencies of 6PGD-A and AGP-S genes decrease.

Differences between generations are also observed in characteristically rare MDH phenotypes; some of them occur only in even-year generations, others only in odd-year generations.

Although with the change of generations, the proportion of heterozygotes at some loci increases and at other loci decreases, the average level of observed (and expected) heterozygosity per individual per locus does not change significantly. It can be noted only that in most pairs of generations the heterozygosity in even years is slightly higher than in odd years, but these differences are statistically insignificant. Such stability of differences between generations implies practically complete isolation between them, at least in the years studied, i.e. the absence of ages other than age 2. The causes of the differences can be accounted for by specific features of the origin and formation of odd- and even-year pink salmon populations during the postglacial period (Aspinwall 1974).

It is probable that the observed differences between the adjacent generations in the allele frequencies at all the loci studied reflect a more profound genetic dissimilarity, which may be a cause of different survival of even- and odd-year pink salmon generations undergoing acclimatization in the north of the European part of the USSR (Dyagilev and Markevich 1979).

3) Population subdivision has proved to be most pronounced in sockeye salmon. We (Altukhov 1974; Altukhov et al. 1975a, b) studied the distribution of genotype and gene frequencies of lactate dehydrogenase (LDG-B^1) and phosphoglucomutase (PGM) in the system of subpopulations of the local sockeye salmon stock of Lake Azabach (polymorphism of these loci in sockeye salmon was described by Hodgins et al. 1969 and by Utter and Hodgins 1970). Lake Azabach sockeye are a typical self-reproducing stock, whose structure has not yet been destroyed by the fishery. Simultaneously, S. M. Konovalov's group studied the biological and ecological structure and estimated the size of individual subpopulations of sockeye salmon in the lake. This stock is composed of several spawning subpopulations that reproduce in different streams and rivers entering the lake ("spring" race) and within the lake at sites near shore ("summer" race). Visual estimation suggests the simultaneous reproduction in Lake Azabach of 30–40 elementary populations. These populations are represented by spawners only, therefore the effective reproductive size (Ne) can be estimated by direct count and by establishing the sex ratio at accessible spawning grounds. Calculated as the harmonic mean, with allowance for sex ratio, the Ne value was about 206 individuals. For six seasons of field work the genetic structure of subpopulations reproducing at 30 spawning grounds has been characterized. Many spawning grounds were studied during several years, therefore we have data on gene frequencies for more than 100 subpopulations isolated from each other in space or time.

The first investigations revealed significant heterogeneity between such subpopulations for the LDH-B^1 and PGM allelic gene frequencies; significant differences in the variance of allelic frequencies persisting through generations were regarded as possible evidence for different selection pressures at these loci. At the same time, the stability of the mean values of gene frequencies and their variances, i.e. genetic stability of the stock as a whole, was demonstrated over the sequence of years studied (Altukhov et al. 1975a).

On the basis of these facts and some other ecological data, we have concluded that the system of subpopulations composing the Lake Azabach sockeye stock is close to Wright's island model (Wright 1951). Therefore, using the corresponding functions describing the distribution of frequencies in a system of subpopulations in a stationary state due to reciprocal equilibrium between systematic and random evolutionary factors, it is possible to estimate the contribution of different population–genetic forces to the maintenance of the observed structure in sockeye salmon and to estimate the fitness of the population with respect to the genotypes of the protein loci studied. We compared the observed distribution of LDH-B^1 and PGM gene frequencies in the subpopulations of the Lake Azabach stock with the theoretically expected distributions inferred from Wright's island model (Altukhov 1974; Altukhov et al. 1975b).

Analysis showed that the observed distribution of PGM gene frequencies differed significantly from the expected stationary one which takes into account only the pressure of migration and genetic drift. However, approximation of the observed and theoretical distributions becomes quite satisfactory if we introduce into the stationary equation a selection factor that takes into account the average intralocus fitness of the population for PGM. The calculation of fitness coefficients (W) of homozygous and heterozygous PGM genotypes gives the following values: $W_{AA} = 0.942$; $W_{AB} = 1.00$; $W_{BB} = 0.822$; i.e. the PGM genotypes are under strong pressure of stabilizing selection acting in favor of heterozygotes. This selection is believed to act at the stage of adult individuals and to follow a selection in favor of homozygotes at the early stages (Kirpichnikov and Ivanova 1977).

Although the real distribution of the LDH-B^1 gene fre-

quencies is satisfactorily described by the theoretical stationary equation that takes into account genetic drift and migration, the introduction into the equation of W values reflecting the pressure of stabilizing selection ($W_{BB} = 0.979$; $W_{BB'} = 1.00$, and $W_{B'B'} = 0.966$) provides a more complete approximation. Later studies and analysis of the LDH-B^1 genotype distribution at spawning grounds of different types indicate a more complicated pattern of selection for this locus. It has turned out that the spring sockeye salmon subpopulations that spawn in streams are subject to a stronger selection pressure than the summer subpopulations adapted mainly to spawning in lakes (Ryabova et al. 1978). A correlation is also observed between the LDH-B^1 allele frequency and water temperature during the spawning period (Titova 1979). Special studies on sockeye salmon revealed the difference in thermostability of the LDH-B^1 allele products, as well as differential mortality of the LDH-B^1 genotypes under elevated temperature and oxygen deficit (Kirpichnikov 1977, 1979). All these facts suggest that selection also plays a certain role in maintaining the LDH-B^1 polymorphism in sockeye salmon, involving such factors as temperature, oxygen content in water at different developmental stages, and probably other environmental factors. The different types of selection-forming polymorphism at the PGM and LDH-B^1 loci, respectively, should be noted. While in the former the selection is universal and determined by some factor common to the whole stock, in the latter the selection intensity (and probably its direction) depends on the type of spawning grounds and therefore cannot be completely estimated using the stationary equation.

4) In 1978, in our laboratory we started population–genetic studies of Atlantic salmon represented by several artificially maintained and natural stocks spawning in the northern European part of the USSR. Differentiation for the IDH phenotype frequencies was discovered between the populations of the Kola, Varzuga, Umba, and Tuloma rivers and, for the malic enzyme phenotype frequencies, between the populations of the Narova and Neva rivers. Most of these populations display genetic subdivision during the spawning run.

Studies of Population Structure in Herring

Population–genetic studies of herring have been started on the basis of the immunogenetic approach. The description of the A-system of erythrocyte antigens in North Sea herring initiated the cycle of work carried out from 1966 till 1975, and covered the territory from the Baltic to the northwestern Atlantic (Altukhov et al. 1968; Truveller and Zenkin 1977a, b).

Hemagglutination reactions (with absorbed rabbit sera, normal sera of man, pig, horse, bovine, lobster, and lectins from lima bean seeds) revealed three phenotypic classes A_1, A_2, and A_0, genetically determined, probably by at least three alleles at one autosomal locus related by successive dominance ($A_1 > A_2 > A_0$). Special tests on parallel agglutination of erythrocytes of the same fish with lobster and human ABO sera demonstrated the identity of the A-system and the C-system of blood groups described by Sindermann and Mairs (1959) in herring: A_0 is identical with the C^- phenogroup, and C^+ includes A_1 and A_2 (Zenkin 1971b). No relation between the phenogroups and age, environmental modification, physiological state, parasitic infection, or hematological pattern of the fish was discovered. In all, more than 16500 herring in 57 samples have been tested in the North Atlantic for the A blood groups (Altukhov et al. 1968b; Zenkin 1966, 1969, 1971a, b, c; 1974; Zenkin and Umnova 1976; Truveller 1971; Truveller and Zenkin 1977a, b). Analysis of A-phenogroup distribution in North Atlantic herring, together with the data on the C^- phenotype distribution, encompasses a 17-yr period of observation. Differentiation stable in time for the frequency of A erythrocyte antigens has been revealed in herring in each of the regions studied (the North and Baltic seas and the northwestern Atlantic). The character of this differentiation is similar in remote parts of the area, and coincides with the pattern of intraspecific ecological subdivision determined by the time and hydrological conditions of spawning of winter–spring oceanic herring (A_1, 100%), summer–autumn marine herring, and spring–summer coastal herring.

Stability of blood group frequencies in time is observed at the level of general populations that coincide with ecological races in herring (Truveller and Zenkin 1977a, b).

Population–genetic studies of herring on the basis of hereditary protein polymorphism revealed by electrophoresis were begun in 1969, when data on the Tf allelic frequencies in spring Baltic and North Sea herring were obtained (Truveller et al. 1973). Most of these studies concerned the distribution of allelic frequencies of several esterases in Atlantic herring (Zenkin 1976; Zenkin and Lysenko 1977; Zenkin and Umnova 1976) as well as the distribution of allelic frequencies of esterases and peroxidases in North Pacific herring (Bogdanov et al. 1979). The general results confirm the concept of hierarchic subdivision of the population system in herring (Truveller 1979). Subdivision into intrapopulational components of different levels in the North Sea herring has been clearly demonstrated (Zenkin and Lysenko 1977), as well as differences for the esterase and peroxidase allele frequencies between Pacific herring elementary populations that spawn in Korf Bay of the Bering Sea (Bogdanov et al. 1979).

For general interpretation of the data of different studies on biochemical genetics of herring, it was important to carry out a direct comparative analysis of geographically remote forms. To this end, the standard method of disc-electrophoresis in polyacrylamide gel was used to investigate the spectra of water-soluble muscle proteins (myogens, esterases, phosphoglucomutase, tetrazolium oxidase, lactate- and malate-dehydrogenases of multivertebrate herring from the Norwegian, North, and Baltic seas, from Georges Bank, shelves of New England and Nova Scotia (410 individuals), and oligovertebrate herring from the Pacific Ocean (Sakhalin) and the White Sea (243 individuals) (Truveller 1979). The Atlantic multivertebrate herring displayed a greater number of alleles, some of its rare alleles being close to fixation in oligovertebrate herring. The genetic distances between the oceanic, marine, and coastal forms of Atlantic herring proved to be similar to that between local populations within the species, whereas the distances between multi- and oligovertebrate herring achieved a level characteristic of different species (corresponding to a time of divergence of 0.5–3 million years). The White Sea herring were found to belong to the oligovertebrate species. Some individuals had alleles

characteristic of Atlantic herring, which can be explained by sporadic hybridization between them, but which does not significantly affect their isolation. Thus, the data of biochemical genetics enrich our knowledge of taxonomic relations between oceanic herrings, which on that basis should be regarded as two species — Atlantic herring (*C. harengus*) and Pacific herring (*C. pallasi*), which includes the White Sea subspecies.

Immunogenetical Study of Intraspecies Differentiation of the European Anchovy Inhabiting the Black and Azov Seas

The European anchovy (*Engraulis encrasicholus*) populations in the Azov and Black Seas were at one time described as the Azov (*E.e. maeoticus* Pusanov) and Black Sea (*E.e. ponticus* Alexandrov) subspecies. In addition to morphological differences, these geographical races vary ecologically. Thus, the Black Sea anchovy is found in that sea throughout the year, but the Azov race only winters there, and migrates to the Azov Sea to spawn and feed. Large schools of anchovy migrating through the Kerch Straits for wintering are objects of an intensive fishery, a practice of long standing. Two questions constantly arise. How many isolated anchovy races are on the spawning grounds, and is it possible that the Black Sea anchovy penetrates to the Azov Sea, thus influencing the abundance of the Azov race?

In addition to certain morphological works, we (Altukhov et al. 1969a, b) conducted immunological studies of the anchovy with the following results.

1) In heterohemagglutination tests with natural (horse and pig sera) and immune (rabbit serum) antibodies, three blood groups were found. These were designated as A_1 (strong reaction with pig and horse serum), A_2 (strong reaction with pig serum, not with horse serum), and A_0 (no reaction with either pig or horse serum).

2) The tests were used to determine differences between the anchovy races. The Azov anchovy possesses all the phenotypes, with the following mean frequencies: A_1, 0.63; A_2, 0.16; A_0, 0.21. The Black Sea race includes only individuals with blood groups A_1 and A_2 (frequencies of 0.9605 and 0.0395, respectively).

3) A detailed analysis of anchovy blood group distribution in the Azov Sea (n = 5936), made from 1963 to 1966, showed the heterogeneous character of the Azov population, which proved to be represented by three subpopulations: Azov proper, part of the Black Sea race which had penetrated there, and a mixed group. The greatest migration of Black Sea anchovies into the Azov Sea was witnessed in 1966.

4) Biological and immunological studies of fish sampled from each trawl disclose a further split of the subpopulations into still smaller, indivisible groups, "elementary populations." Despite the absence of any geographical isolation, these groupings actually differ in respect of frequency of blood groups. Such an isolation has a biological character due to the fact that anchovy spawning is protracted.

We suggest that Naevdal's data on the frequency distribution of hemoglobin and transferrin alleles in sprats, from which "no marked geographical trend could be discovered and in some cases great differences were found among samples from adjacent areas" (1968, p. 178), could be explained by postulating that sprats possess the same kind of "elementary populations" as the anchovy.

Our data indicate that elementary fish populations play an important role in the differentiation and integration of the species gene pool. On the one hand, these populations maintain integrity of self-sustaining races, and on the other, permit gene exchange between them.

Conclusion

We have reviewed 20 years of genetic studies by Soviet authors concerned with the problem of intraspecific differentiation of fish. Although the results of all these works are the same, that is, differences were found among the populations compared, evaluation of the character of the form of divergence shows it to be far from simple in every respect. Thus, whereas the differences in CT, determined to be a species-specific cytophysiological character of poikilothermal animals, may reflect evolutionary changes, the difference in blood group frequencies or certain proteins with low degrees of species-specificity merely attest to group isolation. To prove the evolutionary significance of such variability, a comprehensive and composite approach is essential to be adequate to the complicated problem of speciation.

Thus, two approaches appear valid for solving the problem of intraspecific differentiation of fish: (1) the evolutionary–taxonomic and (2) the population–genetic. Strictly speaking, they naturally cannot be opposed to each other, as the second approach is a new version of the old ichthyological "race" problem that began with Heincke. At the same time, analysis of the gene structure of fish species from the standpoint of population genetics is a separate area for research. We cannot yet always assess the evolutionary significance of population differences in gene frequency. Nevertheless, the recognition and identification of such groupings is critical for understanding the peculiarities of species biology, and consequently for elaborating the scientific foundations of rational fishery management.

From this point of view, the results of our studies deserve attention, because the fish in question clearly show two types of intraspecific groupings, differing in gene frequency. The first type includes "races" or "local stocks" relatively stable over successive generations. The second consists of less stable "elementary populations" that in all probability correspond to Mendelian populations, as mathematically postulated by Wright (1931). Such intraspecific differentiation becomes apparent only from a sufficiently detailed study of the variation of gene frequency in time and space.

At the same time, biological observations clearly indicate a less-marked isolation of elementary populations as compared to spatially isolated communities or "local" stocks. Therefore, elementary populations can be defined as connected populations, and a local stock as a population system. Each elementary population of such a system contributes to the general gene pool of the subdivided population as a whole. It is obvious that only by having regard for the internal organization of such a system and by distributing fishing and management efforts evenly and proportionately over all its components is it possible to have a rational organization of a fish industry that will provide for maintenance of genetic stability of a system of subpopulations over a long series of

generations. If the sometimes variable elementary populations are managed collectively, disregarding their dependent positions in the hierarchic structure of a local stock, the result can only be the disintegration of the population system.

This principle of rational management of genetically subdivided populations has been adopted since 1973 in the work of the Sakhalin chum and pink salmon hatcheries, and has provided a significant economic benefit.

The preservation of hereditary hetrogeneity of fish populations in the course of fishing activity and artificial propagation is the natural basis for efficient management of their stocks.

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Stock Characteristics and Catches of Atlantic Salmon (*Salmo salar*) in Quebec, and Newfoundland and Labrador in Relation to Environmental Variables[1]

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POWER, G. 1981. Stock characteristics and catches of Atlantic salmon (*Salmo salar*) in Quebec, and Newfoundland and Labrador in relation to environmental variables. Can. J. Fish. Aquat. Sci. 38: 1601 – 1611.

More than 500 stocks of anadromous Atlantic salmon (*Salmo salar*) in a natural vigorous state are estimated to exist in Newfoundland and the Quebec–Labrador peninsula. They represent the end result of 6000–13 000 years of natural selection for local conditions and have been subject to relatively little manipulation. Stock characteristics correlating with environmental variables include an inverse relation between smolt age and mean temperature, and smolt age and growing season, and a positive relation between the length of sea life and river discharge. Variations in precipitation and temperature across the area result in different patterns of river discharge. Winter discharge is critically low in the north and salmon are restricted to larger rivers; low summer discharge on the east coast of Newfoundland and in southern Quebec may limit parr territory and hamper adult upstream migration. Because upstream migrations are delayed in years of low rainfall, causing salmon to remain longer in the area of commercial fisheries, salmon catches are generally higher in years of low rain than in wet years. The negative correlation occurs again in the catches of salmon 1, 2, and 7 years after years of low rainfall, but the reasons for this are obscure. Sea and river temperatures confine migration to a very short interval in Ungava and affect life cycles and maturation patterns. Most males spend over 12 mo in freshwater before spawning. Constraints are relaxed further south until high summer temperatures cause selection for early and late running stocks. There is a need for more systematic compilation of salmon stock data particularly over long enough periods to evaluate the effects of climatic variables and management strategies.

Key words: Atlantic salmon, stock characteristics, precipitation and catches, temperature, migration

POWER, G. 1981. Stock characteristics and catches of Atlantic salmon (*Salmo salar*) in Quebec, and Newfoundland and Labrador in relation to environmental variables. Can. J. Fish. Aquat. Sci. 38: 1601 – 1611.

On estime à plus de 500 le nombre de stocks de saumons atlantiques anadromes (*Salmo salar*) dans un état vigoureux naturel à Terre-Neuve et sur la péninsule Québec–Labrador. Ces stocks sont le résultat de 6000–13 000 ans de sélection naturelle par rapport à des conditions locales et ils ont été soumis à relativement peu de manipulation. Parmi les caractéristiques de stocks reliées aux variables de l'environnement, on note une relation inverse entre l'âge des smolts et la température moyenne, et l'âge des smolts et la saison de croissance; on note une relation positive entre la durée de vie en mer et le débit de la rivière. Les modalités de ce débit résultent de variations de précipitation et de température dans la région. Le débit en hiver baisse à un niveau critique au nord, et les saumons sont limités aux grandes rivières; il se peut qu'un faible débit en été sur la côte est de Terre-Neuve et dans le sud du Québec réduise le territoire des tacons et entrave la remontée des adultes. Parce que cette dernière est retardée dans les années de faible précipitation, ce qui force les saumons à demeurer plus longtemps dans les aires de pêche commerciale, les prises sont généralement plus élevées dans les années de faible que dans celles de forte précipitation. Cette corrélation négative apparaît de nouveau dans les prises de saumon 1, 2 et 7 ans après des années de faible précipitation, sans qu'on en comprenne très bien les raisons. Les températures en mer et dans les rivières restreignent la migration à un très court intervalle dans le Nouveau-Québec et influent sur les cycles biologiques et les modalités de maturation. La plupart des mâles passent

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plus de 12 mois en eau douce avant de frayer. Plus au sud, les contraintes sont moins fortes, jusqu'à ce que les températures estivales élevées entraînent une sélection de stocks à montaison hâtive et tardive. En vue d'évaluer les effets des variables climatiques et des stratégies de gestion, on a besoin d'une compilation plus systématique des données sur les stocks de saumons, en particulier sur de longues périodes.

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QUEBEC, and Newfoundland and Labrador are the regions of North America where human activity has had least impact on stocks of Atlantic salmon (*Salmo salar*). Netboy (1974) wrote that "A slower pace of industrialization and settlement, sparser population and the maintenance of many rivers in their natural and wild state, --- have saved a substantial proportion of the original resource." Related to this, salmon management activities have grown slowly because no acute need was apparent.

Interest in Quebec's salmon rivers dates back well over a century to when the first leases for sports fishing were granted. Once influential private interests were focused on sporting use of salmon, management and research became involved in the conflict between commercial and sporting demands on the resource. This continues today with these groups represented by different provincial ministries; Industry, Trade and Commerce for the commercial fishery and Leisure, Hunting and Fishing for the sports fishery. Carter (1964–65) discusses this dispute and makes the point very strongly that private clubs in Quebec have been largely responsible for protecting the resource. "At a time when neither the resources nor the inclination to assume responsibility of management were present from government, these clubs were prepared to undertake the considerable cost necessary for the operation and maintenance of rivers in exchange for exclusive fishing privileges."

New groups have recently entered the conflict by demanding their share, or an increased share, in the salmon harvest. These are the ordinary citizens of Quebec, and Indian and Inuit groups claiming traditional ownership. The recently announced new government policy (Gruenefeld 1980) tries to maneuver a course through this maze of competing interests. It also attempts to address problems of habitat protection and restoration and grapple with the question of priority rights to harvest of anadromous fish by the country of origin. The Quebec government's role in salmon research and management, through time and leading up to the present policy, was reviewed by Côté (1977).

On the island of Newfoundland the history of management has been different. The island has been protected by relative isolation and the salmon resource has been used to support a marginal subsistence economy. Murray (1967) gives an account of the early history of salmon research and management in Newfoundland. Following confederation in 1949, responsibility for the resource passed to the Federal government. Prompted by steadily declining salmon catches, there began a period of stock assessment and marking salmon at sea. This work steadily expanded, moving northwards into Labrador with the tagging work of Blair (1957a, b). In the 1960s renewed interest in salmon stocks was brought about by the continued decline in catches and the threat to salmon stocks posed by the developing Greenland fishery (Saunders et al. 1965; Parrish 1972). This led to the selection of a number of Newfoundland rivers for intensive study of their salmon-producing potential including Western Arm Brook (Chadwick et al. 1978a) and Sandhill River in Labrador (Pratt et al. 1974). A recent description of the Atlantic salmon management program in Newfoundland and Labrador is given by Chadwick et al. (1978b). The record for management in Newfoundland has been generally good, especially during the last decades, when there has been an effort to support and expand natural salmon production (Taylor and Bauld 1972).

In Labrador and the remote areas of Quebec, distance and isolation has meant that nature has been left to take its course. The salmon resources' only protection has been a few difficult-to-enforce regulations and inaccessibility of most of the river headwaters.

The rationale for considering the salmon stocks of these disparate political and geographic regions together is the presumed healthy and vigorous state of the native fish stocks. These stocks have experienced relatively little manipulation either of their habitat or from hatchery plantings, and except for any effects of exploitation, they represent the end results of thousands of years of natural selection for local conditions. Since conditions vary considerably over the area, a logical approach to describing the salmon is to attempt to relate stock characteristics to environmental variables and to speculate on some of the selective variables operating on the natural life cycles.

General Background

Quebec, and Newfoundland and Labrador cover an area of 1 945 206 km^2, about 9% of which is water. The Quebec–Labrador peninsula forms part of the Canadian Shield, the Gaspé Peninsula and insular Newfoundland are part of the Cordilleran rock series, while the Quebec lowlands and Anticosti Island are classified as St. Lawrence lowlands. All the area was glaciated and consists of a flattened plateau of under 1000 m in height dissected by deep valleys with numerous lakes and rivers. Only the Otish mountains in Quebec, the Torngat and Mealy mountains in Labrador, and a few scattered peaks penetrate above the plateau.

Atlantic salmon occur in suitable rivers in the Gulf of St. Lawrence drainage, the Atlantic drainage (except for northern Labrador), and the south Ungava rivers. Outlying stocks exist on the eastern shore of Hudson Bay between Innujuak and Cape Smith. MacCrimmon and Gots (1979) provide a map and more detailed discussion of the distribution. The species occurs in two forms: an anadromous form in coastal rivers, and a 'land locked' form, ouananiche, in the upper reaches of many rivers. Only the better known and economically more valuable anadromous form will be considered in this review. This will simplify discussion, particularly since the detailed distribution and biology of ouananiche is unknown for most

of the area.

An idea of the number of rivers supporting runs of anadromous Atlantic salmon (henceforth referred to as salmon) was obtained from a map of *Atlantic Salmon Rivers of Canada* published by the Atlantic Salmon Association (ASA) 1967, from internal reports of the Atlantic Salmon Review Task Force (1978) and from the *Catalogue of Rivers in Insular Newfoundland* (Porter et al. 1974). By region there are in Quebec approximately: 5 or more in Ungava Bay, 21 in the Lower St. Lawrence, 38 in the upper St. Lawrence, 28 along the south shore of the St. Lawrence and in the Gaspé, and 22 in Anticosti. The number in Labrador is uncertain but is at least 27. There are 222 rivers with records of salmon in Newfoundland. This gives a total of 363+ and, as the larger rivers support a number of tributary stocks, the actual number of anadromous stocks must exceed 500.

Obviously, in an overview of these stocks it would be inappropriate, even if it were possible, to try to describe them individually. Likewise, it has been equally impossible to legislate regulations or manage the stocks individually.

Correlation Between Stock Characteristic and Environmental Variables

An initial analysis to identify relationships between environmental variables and stock characteristics involved compilation of a data bank containing details on climate, location, river size, and period that a location has been available to salmon since retreat of the Laurentide ice sheets. This was done for 152 rivers and coastal fishery districts covering Quebec, and Newfoundland and Labrador. To the extent that information was available, the environmental data were matched with characteristics of the salmon stocks such as smolt ages, sizes, and composition of the spawning runs, timing of the migration, and allele Tf_4 frequencies.

A difficulty was that Atlantic salmon stock data have never been collected or reported in a consistent manner. There are almost no data about most stocks. Data that have been obtained are not always accessible. Scientific publishing policy puts a premium on innovation so that publications address specific and usually different aspects of salmon biology. Data used were therefore extracted from reports and publications available (see appendix). Some data were good, other data were less reliable, while other data were definitely suspect.

Using the SAS program a Spearman correlation coefficient matrix was generated relating 36 environmental variables to 27 salmon stock characteristics. The numbers of matched pairs in each set ranged from 18 to 113. Table 1 reports numbers of comparisons between grouped environmental and stock characteristics in which the null hypothesis that they are not correlated is rejected, using a conservative interpretation, $P < 0.002$.

Most of the correlations revealed by the Spearman matrix were predictable and arise because many environmental variables are arranged on a north–south gradient. An example is smolt age with December precipitation (95 pairs, $P < 0.0002$) which reflects low rainfall and high smolt ages towards the north. Many others relate to temperature being lower, growing seasons shorter, and smolt ages higher towards the north. In this category are correlations relating timing of spawning migration with both precipitation and temperature, the migration being earlier towards the south for reasons discussed later.

Plots of significant ($P < 0.002$) correlations showed that patterns were complex and could not be described by simple regression analysis.

The relationship between latitude and the start of the spawning migration shows that runs start in May and early June in the coastal zones of Baie de Chaleur and St. Georges Bay, SW Newfoundland, but later in the Little Codroy River

TABLE 1. Summary of Spearman correlation coefficient matrix correlating 36 environmental variables with 27 salmon stock characteristics. Summary identifies coefficients where $P < 0.002$.

Salmon characteristics[b]	Environmental variables[a]				
	Precipitation	Temp.	River size	Location	LISR
Run	9	5	—	2	—
% grilse	9	24	4	3	1
Smolt age	18	20	—	2	—
Sea age	1	5	—	1	—
Smolt age by sea age	—	8	—	2	—
Lengths	—	7	—	—	—
Allele Tf_4	—	—	—	—	—

[a]Environmental variables were precipitation: monthly means, annual, and snowfall; temperature: monthly means, growing season length as days with mean temperature above 5.6°C, growing season start, growing season end, date of river freeze over, date river ice free; river size: drainage area, discharge; location: latitude and longitude; LISR: period since retreat of Laurentide ice sheet in 1000 years.

[b]Salmon characteristics were run: peak date of spawning migration, start and end of run; % grilse: percentage of grilse (1-sea-winter salmon) based on Atlantic Salmon Review Task Force, and other publications; smolt ages: mean smolt age, percentages of smolt run of ages 2–7; sea age: percent spawning run by sea winter 1–4, percent repeat spawners; smolt age by sea age: mean smolt age of 1–3 sea-winter and repeat spawning salmon; length: lengths by sea age and mean length of all salmon; allele Tf_4: frequency of Tf_4 allele.

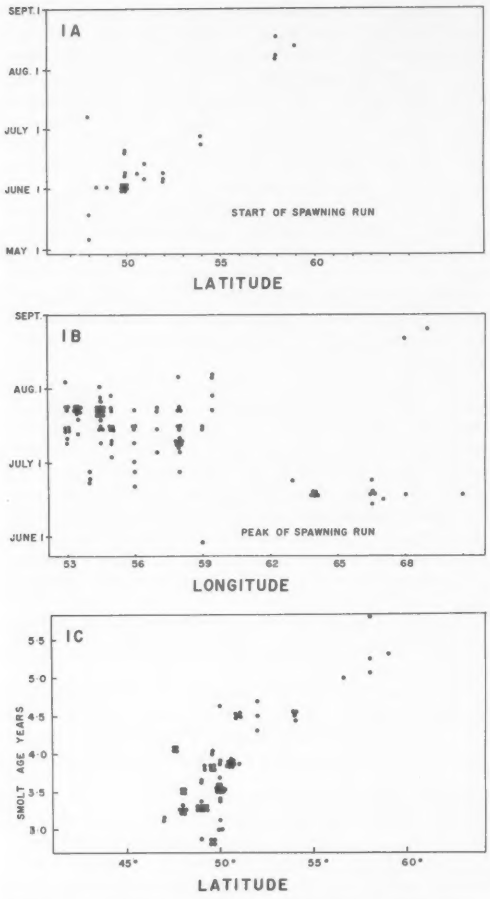


FIG. 1. Some Quebec, and Newfoundland and Labrador Atlantic salmon stock characteristics in relation to latitude and longitude.

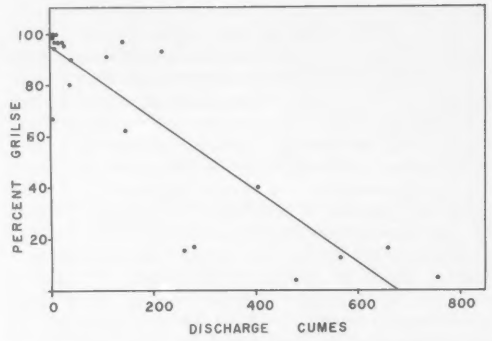


FIG. 2. Percentage of grilse in the spawning run in relation to river discharge for the Bay du Nord, Exploits, Gander, Garia Bk., Garnish, George, Great Rattling Bk., Humber, Larch, Leaf, Matamek, Middle Bk., Moisie, Natashquan, North West Bk., Pipers Hole Bk., Romaine, South West Bk., St. Genevieve, St. Paul, Terra Nova, Whale, White Bear rivers.

at the same latitude. In the Gulf area, between Saguenay and Blanc Sablon, runs occur in early to mid June; Labrador rivers have runs starting at the end of June, while in Ungava spawning migrations are delayed into August (Fig. 1A). When peak periods of upstream migration are plotted against longitude, Newfoundland rivers cluster together with peak runs occurring during July. Runs peak earlier to the west along the Gaspé coast and north shore of the Gulf of St. Lawrence and on the southern Labrador coast. Ungava rivers, at the same longitude as the inner Gulf of St. Lawrence, experience peak runs in late August (Fig. 1B).

Smolts ages increase with latitude in a fairly regular manner (Fig. 1C) and a similar though reversed pattern is produced when smolt ages are plotted against growing season length.

Another gradient across the territory relates to the average size of rivers sustaining salmon populations. These are large in the north; along the Labrador coast and the north shore of the Gulf of St. Lawrence there are many large rivers with some small ones, while on the island of Newfoundland there is a concentration of small rivers. This pattern accounts for the correlations relating the percentages of grilse to precipitation and temperature (which are higher in Newfoundland in winter than elsewhere); for the location and river size correlations; and for the correlation between grilse and time since retreat of the Laurentian ice sheet which occurred early in parts of Newfoundland (Bryson et al. 1969; Prest et al. 1968; Prest 1969).

There is an inverse relationship between the proportion of grilse and river size which is well known to east coast salmon biologists. Correlation coefficients, P values, and pairs of data were for river discharge and two sources of percentage grilse data -0.89, < 0.0002, 18, and -0.83, < 0.0002, and 22. Equivalent values for drainage areas were -0.70, < 0.0002, 27 and -0.75, < 0.0002, and 29. Figure 2 shows the relationship between river discharge and percentage of grilse based on published figures in the literature. Percentage of grilse $= 94.3 - 0.14$ d (d = discharge in cumes (cumes represents rate of river flow in m^3/s)). $r^2 = 0.78$, $F = 69.55$. Schaffer and Elson (1975) described the same association in terms of proportion of grilse and river length.

Graphical methods which include maps provide the best overview of the relationships between stock characteristics and environmental conditions. Figure 3 shows the distribution of smolt ages in relation to the length of the growing season defined as the number of days with a mean air temperature above 5.6°C. Smolt ages used in preparing this figure were obtained from sources listed in the appendix. They are indicative of regional conditions but not exact for each river in a region. The pattern is, however, fairly clear; smolt age is inversely related to growing season length. Symons (1979) showed that, except for the Ungava rivers where smolt size was substantially larger than elsewhere, ~ 500 d with a mean temperature of > 7°C was required to produce the average smolt.

Figure 4 relates climatic variables to stock characteristics for a range of rivers in Quebec, and Newfoundland and Lab-

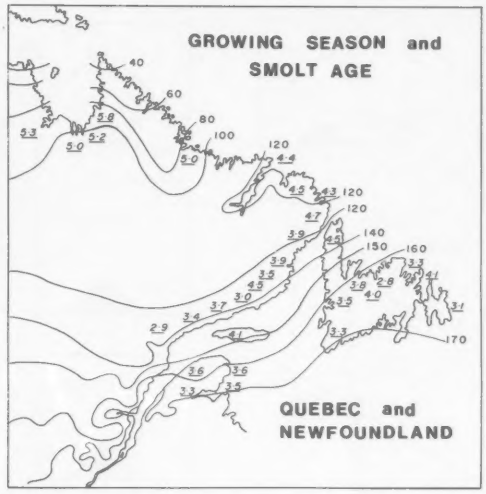


FIG. 3. Mean smolt age in years (underlined) and length of the growing season as number of days with a mean temperature above 5.6°C.

rador. Climatographs for each river give the normal temperature and precipitation curves, the average annual snowfall, and the degree days. The pattern of climatic variation over the region is quite evident with low temperatures, precipitation, and short ice-free period in the north, much wetter and more moderate conditions on insular Newfoundland and southern Quebec. The salmon stock characteristics include mean smolt age (in years), fork length (in centimetres), proportions of different aged smolts; fork lengths (in centimetres), proportions and sex ratios of 1 sea-winter, 2 sea-winter, 3 sea-winter, and repeat spawning salmon. The rivers represented range from large: Koksoak, Moisie, Cascapedia; intermediate: Humber, Gander, Sandhill; to small: Jupiter, Corneille, Little Codroy, S.W. Brook. Between them they cover the range of variation found in climate and salmon stocks across the area. Salmon stock characteristics show no simple pattern being influenced by river size as well as climate. Large rivers show a predominance of large multi-sea-year salmon and repeat spawners; an exception is the Ungava rivers, where high average ages of smolts might limit the duration of sea life, and factors relating to maturation and migration, described later, must reduce the chance of repeat spawning. Smolt ages vary, being lowest in SW Newfoundland and generally increasing northwards. Smolt sizes are fairly consistent, increase slightly on the Labrador coast and markedly in Ungava Bay. Grilse tend to be all or predominantly male on the north shore of the Gulf of St. Lawrence; in parts of Newfoundland and Anticosti Island sex ratios may be even, or the ratio may favor females as in the Gander and Humber rivers.

River Flows and Critical River Conditions

The considerable changes in precipitation, snowfall, and temperature across Quebec, and Newfoundland and Labrador have a direct effect on river discharge. It is well known that river flows have an effect on fish stocks. Attention is largely directed to the question of maintaining stream flows in the face of water abstraction for industrial, domestic, and agricultural use. Instream Flow Needs was the subject of a recent AFS specialty conference (Orsborn and Allman 1976) which tended to emphasize the many legal and administrative aspects of the question.

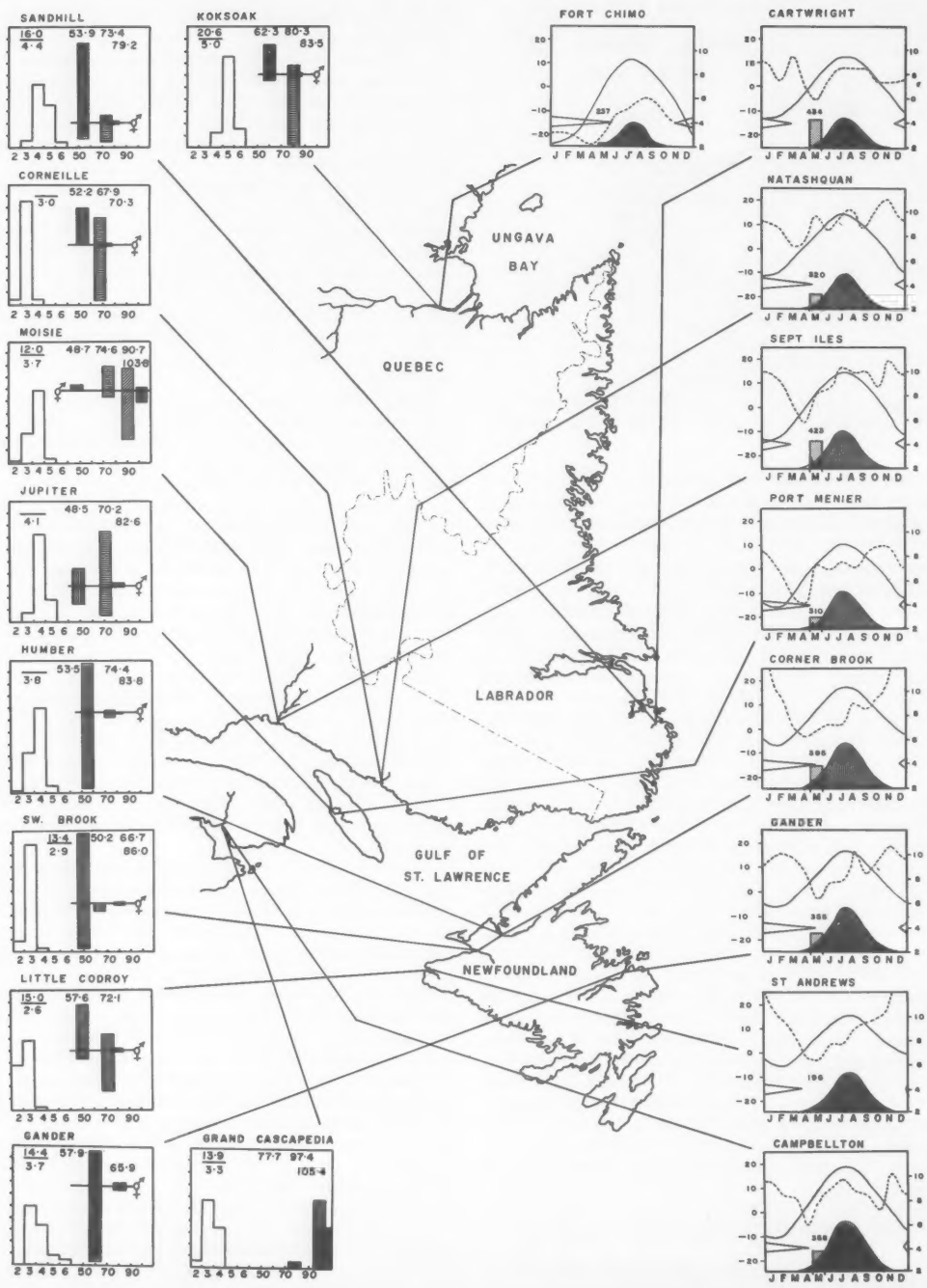
Biological effects of flow reduction are complex, and efforts are being made to find out how much water can be removed from rivers while still maintaining adequate fish and aquatic invertebrate habitat. A practical answer has been provided by application of the "Montana Method" (Tennant 1976) and this indicates that below a 20% average flow in winter, or 40% in summer, habitat deteriorates and degradation is accelerated as flows are reduced. Similarly, high flows can have devastating effects especially in unstable eroding substrates.

Monthly flow patterns for some Quebec and Newfoundland rivers are given in Fig. 5, and flows are expressed as mean flow coefficients (MFC) to facilitate comparisons. The George, in Ungava, and the Eagle, in Labrador, show very low winter MFC's and late spring runoff with good summer flows above or close to the annual average MFC. The 0.2 MFC winter flow criteria of the 'Montana Method' would suggest these rivers suffer habitat deterioration during winter months and that, apart from any other considerations, this is the critical time of the year for salmonids. This correlates with the observation that salmon appear to utilize the main rivers and avoid all except the largest tributaries of the Ungava rivers for spawning and nursery areas.

Winter flows are higher and spring runoff earlier in the Moisie, Des Rapids, and Nabisipi rivers along the north shore of the Gulf of St. Lawrence. Along this coast summer flows may approach 0.4 MFC in the small rivers (Des Rapids and Nabisipi), but are unlikely to do so in large systems. Spring is earliest in the southern Quebec rivers like the Matane and Cascapedia. In this region, winter flows are adequate, but summer flows approach the critical 0.4 MFC in small rivers like the Matane.

Climatic patterns on the Island of Newfoundland produce high winter flows, and late and rather protracted spring runoffs; but problems are likely to arise in some of the smaller rivers in dry summers. The Torrent River on the northern peninsula maintains good summer flows, as does Harrys River on the west coast, but both the Gander River, on the east coast, and Grey River, in the south, can suffer from low summer discharges. During the 27-yr period 1950–76 the Gander River experienced mean monthly summer flows < 0.4 MFC during 49 months and < 0.2 MFC in 19 months, the lowest flows generally occurring in August or September (Historical Stream Flow Fish. Environ. Can., 1976). A similar pattern during a shorter period of observation (8 years) appears to apply to Grey River. If minimum daily flows are considered, flows < 0.1 MFC occur about every 4th year in the Gander River. These flows will drastically reduce parr habit and limit salmonid production in these rivers.

Where anadromous fish are involved there is the added necessity of flows suitable for migration. The most comprehensive work in this topic has been carried out by the Lancashire River Authority (Stewart 1972). For adult upstream


SANDHILL
16·0 53·9 73·4
4·4 79·2
2 3 4 5 6 50 70 90
KOKSOAK
20·6 62·3 80·3
5·0 83·5
2 3 4 5 6 50 70 90
FORT CHIMO
237
J F M A M J J A S O N D
CARTWRIGHT
434
J F M A M J J A S O N D
CORNEILLE
3·0 52·2 67·9
70·3
2 3 4 5 6 50 70 90
NATASHQUAN
320
J F M A M J J A S O N D
MOISIE
12·0 48·7 74·6 90·7
3·7 103·6
2 3 4 5 6 50 70 90
SEPT ILES
423
J F M A M J J A S O N D
JUPITER
4·1 48·5 70·2
82·6
2 3 4 5 6 50 70 90
PORT MENIER
310
J F M A M J J A S O N D
HUMBER
3·8 53·5 74·4
83·8
2 3 4 5 6 50 70 90
CORNER BROOK
395
J F M A M J J A S O N D
SW. BROOK
13·4 50·2 66·7
2·9 86·0
2 3 4 5 6 50 70 90
GANDER
385
J F M A M J J A S O N D
LITTLE CODROY
15·0 57·6 72·1
2·6
2 3 4 5 6 50 70 90
ST ANDREWS
196
J F M A M J J A S O N D
GANDER
14·4 57·9
3·7 65·9
2 3 4 5 6 50 70 90
GRAND CASCAPEDIA
13·9 77·7 97·4
3·3 105·4
2 3 4 5 6 50 70 90
CAMPBELLTON
388
J F M A M J J A S O N D
UNGAVA BAY
QUEBEC
LABRADOR
GULF OF ST. LAWRENCE
NEWFOUNDLAND

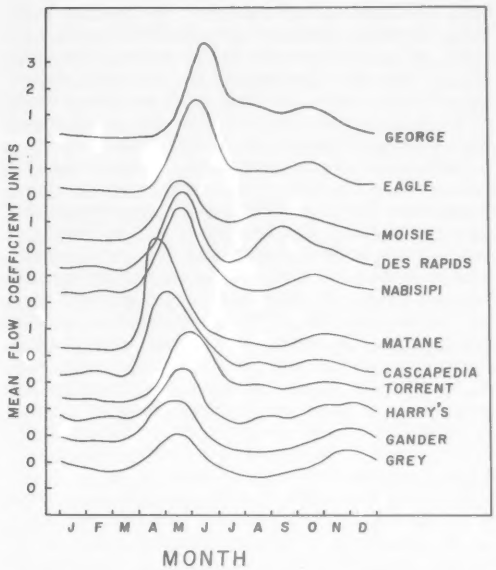


FIG. 5. Mean flow coefficients for some Quebec, and Newfoundland and Labrador rivers. An MFC of 1 equals the mean annual discharge rate. Zeros on the vertical scale represent the no-flow condition for each of the 11 rivers shown.

migration a maintained flow above 0.09 cumes m^{-1} river width is required to initiate movement, migration peaks at about 0.2 cumes m^{-1} width, while salmon migration stops during flood conditions.

Data for five unregulated flow-gauging stations on rivers in Newfoundland and Labrador show that flows as low as 0.2 MFC provide between 0.11 and 0.30 cumes m^{-1} width. Only during extreme low flows does the volume of water passing the stations fall below the 0.09 cumes m^{-1} required to initiate migration. During dry summers, conditions for migration are suboptimal in some insular Newfoundland rivers and the same would almost certainly apply to streams on the Gaspé peninsula and the island of Anticosti in Quebec.

Rainfall and Salmon Catches

The pattern of river flows suggests that precipitation might have an effect on salmon catches by influencing production of young in the rivers. A second possible interaction could be with commercial catches taken in home waters; dry years with low summer flows delaying salmon entry into rivers and increasing the catch, with the opposite occurring during wet years. An analysis of rainfall and salmon catches was undertaken to test the hypothesis that rainfall is correlated with commercial salmon catches either in the year of the catch, or after a lag period, depending on the stage of the life cycle influenced by the precipitation.

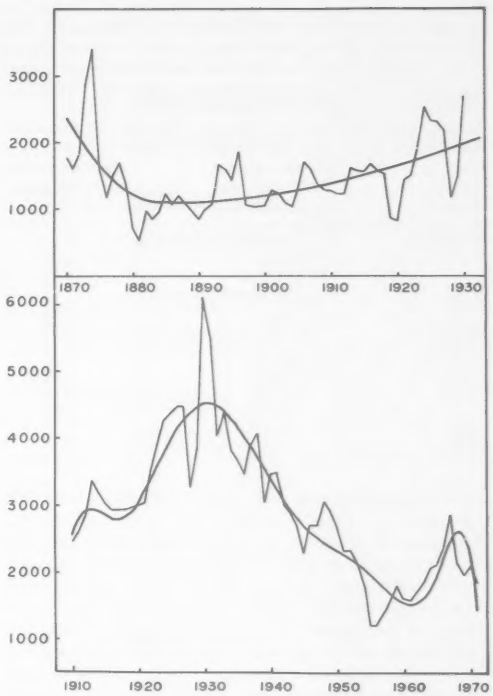


FIG. 6. Commercial salmon catches (kg × 1000) for the Maritimes, 1870–1930 (*upper panel*) and for Eastern Canada 1910–1971. Polynomial trend lines, fitted to each set of catch statistics, are shown. These were used to estimate deviations in the annual landings from the trend lines; these deviations were correlated with precipitation data as explained in the text.

Salmon catch statistics are available for about 100 years. The earlier records apply to the Maritime area and were collected and analyzed by Huntsman (1931). He came to the conclusion that solution to the problem of varying catches (and abundance) of Maritime salmon required more information and extensive investigation. He described a 9.6-yr

FIG. 4. Salmon stock characteristics and climate of Quebec, and Newfoundland and Labrador. The salmon stock diagrams have a vertical scale in 10% units; the horizontal scale is in years on the left and centimetres on the right. The percentages of different aged smolts are on the left with the mean age (yr) and fork length (cm) above. Percentages of adults by sea age and spawning history are on the right; males are above, females below, the horizontal dividing line; vertical shading — grilse, horizontal shading — 2 sea-winter, diagonal shading — 3 sea-winter, and solid shading — repeat spawners. Mean fork lengths (cm) of maiden fish, by sea age are given along the top right; repeat spawners below. Climatographs for each stock location give mean monthly temperature (°C) solid line, left vertical scale; mean monthly precipitation (cm), broken line, right vertical scale; growing season in mean monthly degree days above 5°C, right vertical scale minus 2 in 100 degree days, vertical shaded area; snowfall (mm), right vertical scale × 100 stippled area plus total above March; ice cover is indicated by triangular points on sides of the climatographs.

TABLE 2. Correlation coefficients (r) between rainfall indices for the Maritimes 1872–1930 and deviations from Huntsman's 1930 Maritime salmon catch statistics trend line and for eastern Canada 1910–71 and deviations from Canadian Atlantic salmon catch statistics trend line 1910–71 for lag intervals to 10 years. Values of r where $P = <0.05$ indicated by *.

Rainfall index lag period (yr)	(r) Maritime salmon catch deviations 1872–1930	(r) Canadian salmon catch deviations 1910–71
0	−0.21	−0.24
−1	−0.23	−0.36*
−2	−0.41*	−0.38*
−3	−0.17	−0.20
−4	−0.18	−0.08
−5	−0.17	−0.11
−6	−0.14	−0.22
−7	−0.23	−0.25*
−8	−0.17	−0.21
−9	−0.23	−0.23
−10	−0.24	−0.23

depression in abundance and compared this periodicity with that shown in catches of many furbearing animals. He suspected a 48-yr cycle of abundance, and he noted that small rivers were more susceptible to depletion than large, probably because of accessibility for poaching. Recent statistics have been collected by the federal Department of Fisheries and Oceans or the Quebec government. Methods of collection are described in the 'Harvesting the Resource' report of the Atlantic Salmon Review Task Force (1978), which provides historical catch data from 1910 to 1977. After 1971, catches were reduced in the Maritimes and parts of Quebec as a result of the ban on commercial fishing in those areas, designed to protect heavily depleted stocks. Newfoundland dominates the catches, accounting for about two-thirds of the total. Fluctuations in abundance are synchronous for all areas which, in order of size of catches, are Newfoundland, New Brunswick, Quebec, and Nova Scotia. This suggests that conditions influencing salmon catches act simultaneously on all salmon stocks. Climatic variable(s) acting on either the river or marine environment or biological factor(s) modifying marine growth or survival could be responsible.

Precipitation data for eastern Canada were provided by the Atmospheric Environment Service for eight locations: Fredericton, N.B.; Halifax, N.S.; Charlottetown, P.E.I.; Cornerbrook, St. John's, and Goose Bay, Nfld.; Anticosti and Fort Chimo, Quebec. A rainfall index for eastern Canada was calculated using the percentage deviation from the sum of the long-term means for annual rainfall, from the sum of rainfall recorded for stations reporting in any year. The index goes back to 1872. In 1873 only one station was available; in 1872 and 1906, two stations; for 5 years there were three stations, in all other years four or more. The record is most complete after 1913 when records from up to five of the eight stations were available, and it is best after 1948. A similar index was calculated for the Maritimes using the records for the three Maritime locations.

Trends apparent in the commercial salmon catch data for the Maritimes 1872–1930 (Huntsman's 1931 data) and for eastern Canada 1910–1971 (Atlantic Salmon Review Task Force 1978 data) are high catches in the Maritimes in the 1870s followed by a period of generally lower catches in the 1880s, and a gradual recovery to high catches in the 1920s (Fig. 6). The eastern Canadian catch shows a parallel increase from 1910 to a peak in the early 1930s and then a steady decline to landings of about a third the peak period around 1960. There is a slight recovery to 1967, then a decline.

Catch statistics from an area as large as eastern Canada, for a diffuse fishery that is partly subsistence, are subject to many uncertainties. Huntsman (1931) went to some lengths discussing the reliability of his figures and concluded, because of parallel trends between districts, that they were a reliable index of abundance. Recent statistics are probably more reliable and accurate. Considering the overall pattern of landings: the increase to the 1930s can be related to increased participation in the fishery, improvements in gear and its operation, and more accurate and complete reporting of catches. The post-1930 decline has been caused by: gradual degradation and losses of habitat brought about by forestry, agricultural and industrial activity, and population growth. Recent catches are being reduced by overexploitation of a declining resource (Paloheimo and Elson 1974).

To remove these trends from the data, polynomial curves were fitted and deviations from these were correlated with a rainfall index for the Maritimes, Huntsman's data, or for eastern Canada, 1910–71 catch data (Fig. 6). Best fit to the early data was a 5th-order curve, $r^2 = 0.37$, F ratio 6.15, and for the more modern data a 10th order curve $r^2 = 0.80$, F ratio 19.90.

Table 2 gives the results of correlation analysis, comparing rainfall indices with deviations of catch from the salmon curve trend lines for lag periods up to 10 years. For both sets of data all correlation coefficients are negative and there is a consistent pattern in the values, with strongest correlations occurring in the year of the catch, and with lags of 1, 2, and 7 years. For the modern data in the year of the catch, the r value is just short of the critical value of 0.250 for $P = 0.05$. However, a χ^2 test (with Yates correction), comparing rainfall above or below normal, and salmon catch above or below the polynomial trend curve shows a significant association ($\chi^2 = 7.82$ $P = 0.005$) between higher than expected salmon catches and lower than average rainfall. For the 1-, 2- and 7-yr lag periods, $P = < 0.05$. In the earlier data the correlation coefficients are not quite so strong, except for the 2-yr lag period which has a $P = < 0.01$.

The correlation between rainfall and salmon catch the same year relates to the ease with which salmon approaching the coast enter the rivers, thus escaping the fishery in years of high rainfall, and presumably high river flow, and the delays that permit higher catches in coastal fisheries in years of drought. The correlations at 1- and 2-yr lag periods can only relate to factors affecting smolt output. The association calls for higher than normal smolt output in dry years and lower than normal in wet years. This effect must be sufficiently great to be carried through and affect the numbers of grilse returning 1 year later, and the number of 2-sea-winter fish 2 years later. Chadwick et al. (1978a) found a highly significant relationship between smolt output and the number of grilse returning 1 year later to Western Arm Brook, an all-grilse river in Newfoundland. Paloheimo and Elson (1974) showed a highly significant relationship between smolt output and

salmon landings 2 years later for the New Brunswick catch dominated by 2-sea-winter fish. A carry-through effect, therefore, is reasonable and supported by evidence in the literature.

How rainfall could affect smolt output or survival is speculative. The action may be simply one of reduced space in dry years, subsequent crowding of the habitat inducing more fish to migrate seawards. This effect must operate early in the year to influence smolt migration, i.e. before much of the year's rainfall had occurred.

Similarly, discussion of the 7-yr lag effect is even more speculative. The following hypothesis might be proposed. In high rainfall years more salmon escape the fishery (the 0-yr lag effect), enter the river early, and penetrate far upstream to spawn. The following year headwaters, tributaries, and mainstream are well stocked with fry. Progeny of fish entering to spawn that year produce young which have to compete for space with a successful and well-distributed previous year-class, and their survival is depressed. Because the major component of the salmon catch is aged 5+ (6 yr), this leads to a depressed catch 7 years after the high rainfall year. It would also be expected to lead to a high catch 6 years after the high rainfall year which, if it occurred, would eliminate the negative correlation coefficient with the 6-yr lag. It might also dampen the negative correlation coefficient a year later (7-yr lag) because some smolts from a strong-year-class would be expected to migrate at age 4+ and any grilse which survived to spawn a second time would return in the 7th year. That this does not occur implies that the strong-year-class is reduced before smoltification, and this could occur in any low rainfall year prior to seaward migration by restricting the rivers' carrying capacity. The net result is the productive capacity of each river pulses with rainfall in a complex manner which affects smolt output. This is correlated with adult returns 1 and 2 years later, and an average generation effect that gives rise to negative correlations between catches and rainfall 7 and more years previously. A test of part of this hypothesis would be to see if smolt ages declined in dry years, which would indicate crowding was displacing more young fish seawards under these conditions.

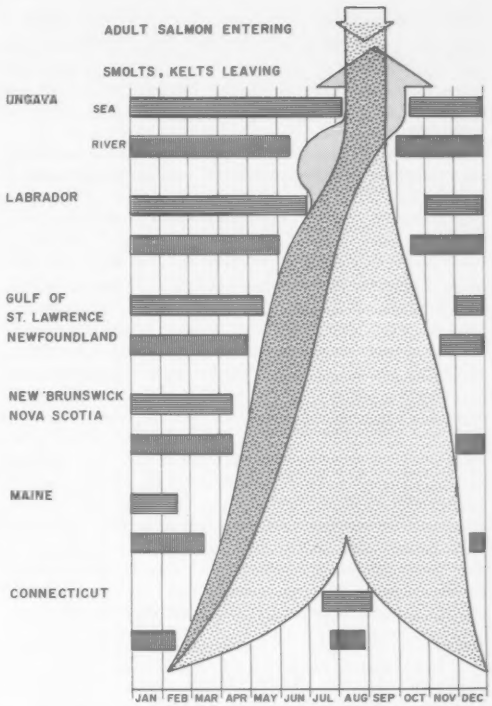


FIG. 7. Constraints to movement of Atlantic salmon imposed by sea and river temperatures. Unsuitable sea temperatures are indicated by horizontal shading, unsuitable river temperatures by vertical shading. Note that in Ungava there is a very short period for free movement when both sea and river temperatures are favorable. In the south summer temperatures begin to affect movement and there is selection for early and late running stocks. Maine and Connecticut stocks, 12 000-15 000 yr ago, would have been subject to similar restraints to movement as Ungava and Labrador stocks today.

Temperature Constraints on Movement

Atlantic salmon migrate only within certain ranges of temperature. The threshold for smolt migrations seems to be between 7 and 10°C. When these temperatures are attained in spring, migration occurs, often peaking soon after or along with a freshet. Adult salmon enter east coast rivers mostly during summer months when water temperatures are high. Stewart (1972) observed that salmon migrate upstream most frequently when air temperature is lower than that of river water. It is uncertain what temperatures will delay or stop salmon movement in freshwater, probably those above 22°C (Gibson 1966). Kelts move seawards after spring runoff when water temperatures exceed 4°C. Observations on the timing of the arrival of salmon in coastal waters indicates that they avoid sea of temperatures below 2°C (Lear, quoted in Lee and Power 1976). May (1972) reported few captures of salmon below 2°C, and most west Greenland feeding salmon concentrated in waters between 3 and 8°C.

Using this information, combining it with maps of average sea surface temperature, and assuming that river temperatures follow mean air temperature fairly closely, it can be shown that migration timing has to be very precise in the north, and constraints to movement are relaxed as climatic conditions become moderate until, in the south, limits are imposed again by river and sea temperatures that are too high.

The simplest example to describe is perhaps the most informative. The Ungava rivers reach temperatures suitable for smolt migration in June, and the migration peaks in the lower reaches of the rivers in July (Power 1969). When the smolts and the kelts that have descended with them enter the estuaries, they encounter very low temperatures, and the migration is delayed until August when surface sea temperatures finally reach 2−4°C in Ungava Bay (Dunbar 1958). Many smolts remain in the estuary all summer and are still there in September and October, at which time they have attained lengths of 30−35 cm and weights of 500 g. At this time the differential between river and sea temperatures disappears, or is reversed, and most smolts have left Ungava Bay. A few remain, some years more than others, and these fish over-

winter in the estuary or freshwater and show, as a result, a very clear winter check on their scales. Power (1980) reported that the percentage of such fish among returning 2-sea-winter fish, taken in the fishery at Fort Chimo, varied from 0.8 (1964) to 12.0 (1979) during 10 years of sampling, 1961–69 and 1979.

The return migration of adult salmon arrives in the estuaries coincidently with the attainment of suitable temperatures in Ungava Bay. Time of arrival of these fish varies from year to year depending on ice and wind conditions (Power 1976). Two-sea-winter salmon, 70% female, arrive on average a week to 10 days ahead of 1-sea-winter fish, which are 85% male. About 5% of the females and 85% of the males have immature gonads. Mature fish spawn in the fall when they enter the rivers, the remainder remain in freshwater over 12 mo before their gonads ripen. This mechanism is an adaptation to late arrival of fish at the river mouth, controlled by sea temperatures, and a short period of temperatures suitable for migration and maturation once the fish enter the rivers.

Figure 7 summarizes this description and shows schematically how constraints on movement vary with latitude. Similarly, since conditions now found in Ungava Bay must at one time have existed further south, the figure can be used, along with an estimate of the paleoclimate since postglacial colonization, to show how these constraints have changed in time. Selection pressures change with conditions, and a maturation cycle, such as has been described for a proportion of Ungava salmon, may be a considerable disadvantage under more benign climatic conditions, and in smaller rivers.

Conclusions

In summary, with the presently available information, the salmon stocks of Quebec, and Newfoundland and Labrador might be divided into five groups. The Ungava Bay stocks show many distinctive characteristics including large, old smolts and maturation cycles that involve a proportion of the fish returning to the rivers more than a year before spawning. The Labrador stocks exhibit high smolt ages, normal-sized smolts, and mixed grilse and 2-sea-winter runs; grilse are mostly male and larger fish mostly female. The north shore Gulf of St. Lawrence stocks have lower smolt ages, and grilse are almost all male. Newfoundland stocks have a high proportion of grilse and grilse sex ratios can be even. A fifth grouping might be Anticosti and the Gaspé, with lower proportions of grilse of both sexes and lower smolt ages. Within all regions the proportion of grilse increases in small rivers, and large 3-sea-winter salmon are confined to big rivers in Quebec, outside of Ungava Bay.

The stocks of the area cannot be classified as neatly into groups as those of Europe were by Payne et al. (1971) into 'Boreal' and 'Celtic' races, whose history and isolation could be related to glacial events. It is more likely that variations in stock characteristics are of adaptive significance and fit into patterns like those outlined by Schaffer and Elson (1975). There is, however, a shortage of detailed published information about stocks, most of which remain undescribed. A policy of obtaining such information, especially over a period of time, would probably pay large dividends. It would help us understand the complexities of population dynamics as discussed in the section on rainfall and salmon catches. It would be particularly useful in showing how selective exploitation has changed stock characteristics, as it surely has. It would show clearly why some rivers, like the smaller north shore Gulf of St. Lawrence rivers, are particularly vulnerable to damage from overexploitation of the larger female component of the stocks. Finally, such information must be obtained to record the effects of environment change, be it habitat rehabilitation for management or degradation from varied causes.

Acknowledgments

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Atlantic Salmon (*Salmo salar*) Stocks and Management Implications in the Canadian Atlantic Provinces and New England, USA[1]

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SAUNDERS, R. L. 1981. Atlantic salmon (*Salmo salar*) stocks and management implications in the Canadian Atlantic Provinces and New England, USA. Can. J. Fish. Aquat. Sci. 38: 1612–1625.

This paper discusses the diversity of Atlantic salmon (*Salmo salar*) expressed as anatomical, physiological, and behavioral differences among stocks in the Atlantic Provinces of Canada and New England, USA. Evidence is reviewed for environmental and genetic influence on a number of stock-specific traits. Unique qualities of particular stocks are described. The loss of salmon from much of its former range is documented and discussed in relation to stock characteristics important in rehabilitation efforts. The mixed stock fisheries in Greenland and Newfoundland are considered from the point of view of interception. It is concluded that identification and management of specific stocks in the Greenland fishery are impracticable at present but that identification of North American components, using discriminant function analysis of scale growth patterns and smolt tagging, should be continued. In Newfoundland knowledge gained from tagging studies allows a significant degree of management of stocks from mainland Canada together with those from Newfoundland and Labrador. Since it is impracticable now to manage the fisheries off Greenland and Newfoundland and off the major Canadian Maritimes salmon-producing rivers — the Miramichi, Restigouche, and Saint John — in strict recognition of stocks, it is suggested that it may be possible to characterize an assemblage of like stocks from given areas and to identify and manage for these in large mixed-stock fisheries. Possible impacts of hatchery plantings are discussed in relation to prospects of success and effects on native stocks. It is concluded that we have the biological basis for evaluating likelihood of success and degree of danger to native stocks from extensive plantings of hatchery-reared juvenile salmon and that such evaluation should be conducted when embarking on projects involving use of hatchery-reared fish as part of a major salmon enhancement program in Atlantic Canada.

Key words: genetics, environmental influence, rehabilitation, enhancement, interception, hatcheries, aquaculture

SAUNDERS, R. L. 1981. Atlantic salmon (*Salmo salar*) stocks and management implications in the Canadian Atlantic Provinces and New England, USA. Can. J. Fish. Aquat. Sci. 38: 1612–1625.

Ce qui suit est une analyse de la diversité observée chez le saumon atlantique (*Salmo salar*) et qui s'exprime par des différences anatomiques, physiologiques et éthologiques entre les stocks des provinces atlantiques du Canada et de la Nouvelle-Angleterre (É.-U.). On y passe en revue l'information relative à l'influence que l'environnement ou l'hérédité peut avoir sur plusieurs caractères spécifiques au stock, et l'on décrit les qualités uniques de stocks particuliers. On documente et analyse la disparition du saumon d'une bonne partie de l'aire qu'il occupait jadis, par rapport à certaines caractéristiques de stock susceptibles de jouer un rôle important dans la réhabilitation. L'aspect interception dans les pêcheries de stocks mixtes du Groenland et de Terre-Neuve est analysé. On en vient à la conclusion que l'identification et la gestion de stocks spécifiques dans la pêcherie du Groenland sont présentement irréalisables. Par contre, l'identification des composants nord-américains, par analyse discriminante des caractéristiques de croissance des écailles, devrait se poursuivre. À Terre-Neuve, grâce aux connaissances acquises à la suite d'étiquetages, les stocks du Canada continental peuvent être gérés jusqu'à un certain point avec ceux de Terre-Neuve et du Labrador. Puisque,

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pour le moment, une gestion de la pêche au large du Groenland et de Terre-Neuve, et au large des principales rivières à saumon des Maritimes — Miramichi, Restigouche et Saint-Jean — fondée sur une identification précise des stocks, est irréalisable, on pourrait peut-être définir les caractéristiques d'un groupe de stocks identiques d'une région, et gérer ce groupe comme stock mixte. Nous examinons les répercussions possibles de peuplements de poissons d'élevage sur leur chance de réussite ainsi que sur les stocks indigènes. Nous concluons qu'on possède le fondement biologique suffisant pour évaluer les chances de succès et le danger, à l'endroit des stocks indigènes, de peuplements massifs de jeunes saumons d'élevage. Une telle évaluation devrait se faire au moment de la mise en marche d'un programme d'envergure de mise en valeur du saumons dans l'Est du Canada, impliquant des peuplements de poissons d'élevage.

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ATLANTIC salmon (*Salmo salar*) show great diversity in respect to anatomical, behavioral, and physiological characteristics (Saunders and Bailey 1980). The obvious diversity among typical salmon types from different rivers results from both genetic and environmental influences and is explainable on the basis of stock differentiation. The definition of stock as used in this paper is that given by Ricker (1972). A stock of salmon refers to that group of individuals spawning in a particular stream or part of a stream and not interbreeding to a substantial degree with other such groups spawning in a different place or in the same place at a different season. Thereby, each river has at least one stock of salmon; many medium or large rivers have a number of stocks, one or more in each tributary. The main stem of a larger river may have more than one stock. Homing undoubtedly plays an important part in the differentiation of stocks and in maintaining their integrity.

Management of Atlantic salmon should be in recognition of the stock concept so as to allow for optimum cropping while allowing sufficient broodstock in each breeding population. Recognition of stocks is also important in attempts to enhance existing populations and to establish runs in rivers having no salmon. The objective of this paper is to describe phenotypic and genetic diversity of Atlantic salmon and to review evidence for the existence of stocks from environmental and genetic perspectives. I shall mention some of the stocks that have been lost and describe unique traits that should be considered in restoration and enhancement attempts. Mixed stock fisheries in Greenland and Newfoundland are described and possible management plans are discussed in recognition of stocks. Finally, the effects of a planned salmon enhancement program calling for extensive planting of hatchery salmon are discussed in reference to possible benefit or harm to stocks.

In 1960, when I accepted a position as an Atlantic salmon biologist with the Fisheries Research Board of Canada, the late Professor J. R. Dymond made a prediction which has come to mind repeatedly during the past 20 years with decreasing abundance of Atlantic salmon and stocks being lost because of pollution, obstructions to upstream movement, development of a new highseas fishery, overharvesting, and, most recently, acidification of rivers. He warned that I would probably see the end of the Atlantic salmon as a self-sustaining species because of habitat destruction and overharvesting. He added that there would continue to be "museum-type" or domesticated populations of salmon. This presentation concerning phenotypic and genetic variability of salmon, loss of genetic diversity, salmon management in recognition of stocks, and effects of hatchery introductions is made with Professor Dymond's prediction in mind.

Phenotypic and Genotypic Diversity

Many fishery biologists have attributed obvious differences among salmon from different rivers largely or entirely to environmental influences. Recently, it has been accepted that both environmental and genetic factors are responsible for these, and more subtle, differences among stocks of salmon. In a paper on early and late runs of salmon in the Northwest Miramichi (Saunders 1967), genetics was not implicated. It was suggested that environmental differences between upper and lower stretches of the river resulted in early and late entry with the size difference between the two components (Saunders and Allen 1969) owing to growth between early (June–July) and late (September–October) entry (Fig. 1). However, Møller's (1970) data on transferrin patterns indicated that there were genetically distinct populations in the upper and lower reaches of the northwest Miramichi, and thus genetics is implicated in the size differences. Ricker's (1972) comprehensive review and documentation of genetic and environmental influence on Pacific salmonid stocks and the recent work of Ståhl (1980) leave no doubt about the genetic basis for salmon stocks.

In comparison with the abundant data reviewed by Ricker (1972) for Pacific salmonid stocks, there is a scarcity of such data for North American Atlantic salmon. Møller (1970) conducted the first systematic study leading to the identity of Atlantic salmon stocks in North America. He sampled runs of salmon from Maine to Labrador (Fig. 2) for transferrin alleles and found genetic diversity and genetic differences between populations. Møller's data suggested restricted migration between spawning localities. He identified three groups of salmon, based on transferrin alleles: Labrador and Newfoundland, New Brunswick and Nova Scotia, and Maine. Samples from larger rivers, the Miramichi and Saint John, showed an excess of homozygotes, and this finding was the basis for suggesting subdivision into smaller groups. Although there has been considerable transplantation through release of hatchery-reared fish, particularly in the Maritime Provinces and Maine, there appears to have been no breakdown of isolating mechanisms with resulting loss of genetic diversity. Møller's study allowed the conclusion that North American Atlantic salmon exist in a number of genetically distinct populations, and it led the way for more detailed

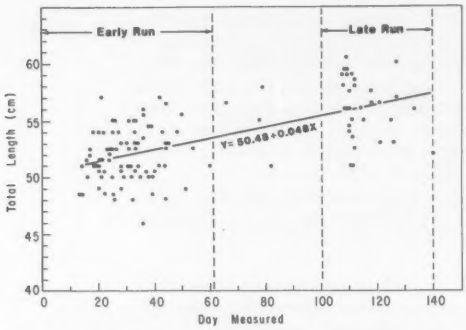

FIG. 1. Relation between total length and date of capture of ascending grilse at Curventon counting fence, N.W. Miramichi River (from Saunders and Allen (1967)).

research to establish stock status.

Foerster (1968) used discriminant function analysis with seven morphological characters to differentiate between stocks of sockeye salmon (*Oncorhynchus nerka*). However, these differences could have been owing to genetic and/or environmental factors. Riddell et al. (1981) combined discriminant function analysis of morphological data with breeding experiments under controlled conditions to give evidence of genetically distinct stocks of Atlantic salmon. They found that growth rate and proximate composition were similar between populations of salmon in two small tributaries, Rocky Brook and Sabbies River (Fig. 3), of the Southwest Miramichi system. In contrast with growth rate and proximate composition, body morphology, as determined by discriminant function analysis, differed significantly between the two populations (Riddell and Leggett 1981). Fish from Rocky Brook had more fusiform bodies and larger fins. Breeding experiments using spawners from the two populations showed growth rates and proximate compositions to be very similar between populations reared under identical conditions (Riddell et al. 1981). However, the differences in body form and fin size observed in naturally produced fish were found to be heritable traits. They concluded that hereditary variation in morphology and a demonstrated directional selection for greater fin size in the high velocity environment of Rocky Brook support a hypothesis that these traits are adaptive (Riddell et al. 1981).

Saunders and Bailey (1980) listed traits which show stock-specific differences in Atlantic salmon. Their listing is updated here (Table 1). Fecundity differs among stocks of anadromous and landlocked salmon (Pope et al. 1961; Baum and Meister 1971), but no study has been done to show relative genetic and environmental contributions to this trait; however, there is a genetic component in egg size among Norwegian salmon stocks (Aulstad and Gjedrem 1973). Survival during incubation and in juvenile stages is influenced by genetics and has a pronounced maternal component (Kanis et al. 1976). Growth rates at various life stages are influenced by genetics (Naevdal et al. 1975, 1976, 1977; Friars et al. 1979), as is precocious sexual maturity in male parr (Saunders and Sreedharan 1977; Glebe et al. 1978). Age at smoltification has a significant genetic component (Refstie et al. 1977). As

FIG. 2. Sample locations for Atlantic salmon transferrin gene frequency studies (from Møller (1970)).

indicated earlier, there is a genetic basis for differences in body form and fin size between stocks (Riddell et al. 1981). There is evidence for genetic control of age and size at sexual maturity (Elson 1973; Naevdal et al. 1976; Ritter and Newbold 1977). We have no data on stock-specific responses to the environmental cue or cues for smolting and to those triggering smolt migration behavior. However, genetic influences are likely in view of different environmental conditions and the requirement for different downstream distances covered by smolts from various stocks. Although differences in migratory behavior at sea have been recognized or suggested for different Atlantic and Pacific salmonid stocks (Ricker 1972; Ritter 1975; Saunders 1977), these observations are difficult to quantify, and estimates of the genetic control of migratory behavior in Atlantic salmon have not been attempted. Seasonal patterns of adult return, the early-late-run phenomenon, have both genetic and environmental bases (Saunders 1967; Elson 1973). Small coastal streams usually have only late runs because of low water conditions during most summers; early runs are usually found in larger rivers or those with lakes, larger bodies of water providing refuge during dry summers. The incidence of multiple spawning is variable among stocks but its hereditary component has not been determined through breeding studies. The Big Salmon River has a high incidence of multiple spawners (Ducharme 1969), like those stocks in some other small rivers entering the inner Bay of Fundy. The high incidence of multiple spawning fish may be related to the fact that most individuals in the Big Salmon River contribute little if any to fisheries outside the Bay of Fundy as they mature as grilse (Jessop 1976; Ruggles and Ritter 1980). Stock-specific resistance to vibrio, a bacterial disease common in marine fishes, was found in Atlantic

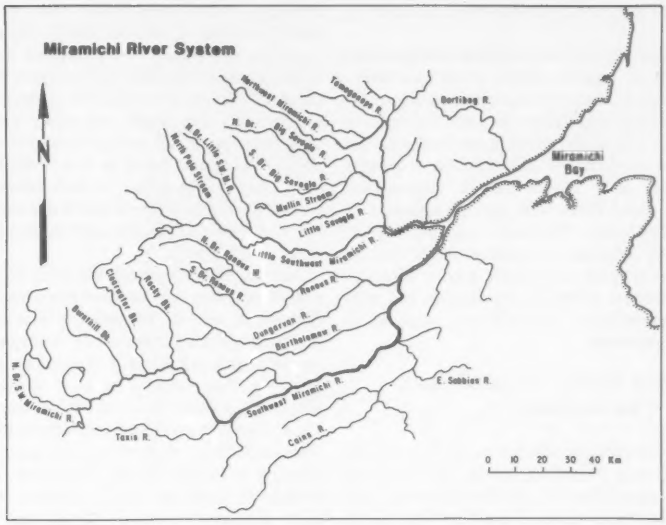

FIG. 3. Miramichi River system showing principal tributaries.

TABLE 1. Traits showing stock-specific differences in Atlantic salmon. (Updated from Saunders and Bailey (1980).)

Trait	References
Fecundity	Pope et al. (1961), Baum and Meister (1971)
Egg size	Aulstad and Gjedrem (1973), Glebe et al. (1979)
Survival to various life stages	Ryman (1970), Kanis et al. (1976)
Rate and patterns of growth	Lindroth (1972), Naevdal et al. (1975), Gjedrem (1976a), Møller et al. (1976), Refstie et al. (1977), Thorpe (1977), Thorpe and Morgan (1978), Bailey et al. (1980), Friars et al. (1979)
Body form	Riddell et al. (1981)
Precocious sexual maturity in male parr	Schiefer (1971), Schaffer and Elson (1975), Thorpe (1975) Saunders and Sreedharan (1977), Glebe et al. (1978)
Age at smolting	Refstie et al. (1977)
Age and size at sexual maturity	Ritter (1972, 1975), Elson (1973), Jessop (1976), Naevdal et al. (1976, 1977, 1978), Ritter and Newbold (1977)
Seaward migration	Gardner (1976), Farmer et al. (1978), Solomon (1978), Riddell and Leggett (1981)
Migratory behavior at sea	Ducharme (1969), Ritter (1975), Jessop (1976), Saunders (1977)
Seasonal pattern of adult return from the sea	Zarnecki (1963), Saunders (1967), Elson (1973)
Multiple spawning	Dymond (1963), Ducharme (1969), Wilkins (1972)
Resistance to disease	Gjedrem and Aulstad (1974)
Resistance to low pH	Gjedrem (1976b), Edwards and Hjeldnes (1977)
Tissue protein and enzyme specificity	Nyman (1967a, b), Møller (1970), Payne et al. (1971), Nyman and Pippy (1972), Wilkins (1972), Beland (1979), Ståhl (1980)

salmon (Gjedrem and Aulstad 1974). Genetically influenced resistance to other serious diseases affecting salmonids — bacterial kidney disease, furunculosis, infectious pancreatic necrosis, and enteric redmouth — has not been determined. Gjedrem (1976b) and Edwards and Hjeldnes (1977) have found some heritability for resistance to low pH in brown trout (*Salmo trutta*), but no such studies have been reported for Atlantic salmon. Atlantic salmon stocks are separable on the basis of frequencies of genes coding for various tissue proteins and enzymes (Nyman 1967a, b; Møller 1970; Payne et

al. 1971; Nyman and Pippy 1972; Wilkins 1972; Elson 1973; Beland 1979).

Breeding studies under controlled conditions have provided unequivocal evidence of genetic control of various traits. There is a need for more detailed electrophoretic studies of the kind done by Møller (1970) and Ståhl (1980) and for breeding studies in combination with observations in the field, like that done by Riddell et al. (1981). The identification of genetic resources was urged at a recent (1980) International Symposium on Fish Gene Pools with special reference to preservation of wild fish stocks. The need is urgent to expand such studies with North American Atlantic salmon to identify existing genetic resources and to maintain genetic diversity while managing the harvest of natural populations, and with due consideration to hatchery breeding and stocking in relation to natural populations.

Loss of Salmon Stocks — Special Stock Characteristics

Atlantic salmon were once abundant from the Connecticut River northwards, through New England and the Maritime Provinces, Quebec, eastern Ontario, and Newfoundland and Labrador. Most of the stocks south of New Brunswick and those from Ontario have disappeared, largely as a result of obstructions and as a result of deforestation, land clearing for agriculture, all compounded and aggravated by pollution. An attempt was made in the mid 1880s to restore a salmon run in the Connecticut River. Salmon were introduced from the Penobscot River in Maine and from New Brunswick and Nova Scotia stocks. Although the effort resulted in some returning adults, the numbers were small and most were taken in fisheries near the river mouth; no breeding population was established. Was this owing to the fact that the brood stock or stocks for the rehabilitation were not native to the Connecticut River and therefore not adapted to that river? About 100 years later a second attempt was begun to re-establish salmon in the Connecticut River using stocks from New Brunswick, Quebec, and the Penobscot River in Maine. Plantings began in the late 1960s and have been as fry, parr, and smolts (Stolte 1980). There have been returning adults but no natural spawning; all of the surviving returns have been used as hatchery broodstock.

The Connecticut River has strict requirements for a salmon run. Long Island Sound and the lower Connecticut are sufficiently warm during midsummer and early fall to preclude entry of adult salmon from the sea. This consideration and experience with transfer of Pacific salmon stocks (Ricker 1972) suggest that stocks which usually return early in the season would have the best chance of entry before waters of Long Island Sound and the lower Connecticut become too warm. Another strict requirement is appropriate timing of smolt runs. In some headwater stocks, the parr large enough to be smolts the following spring move downstream for a certain distance in the autumn and presumably overwinter in some lower reaches of the river (Gardner 1976; Saunders and Bailey 1980). Riddell and Leggett (1981) describe such a stock for Rocky Brook, a tributary of the Southwest Miramichi. They suggest that the habitat is unsuitable for overwintering large parr. Riddell and Leggett observed no emigration of smolts from Rocky Brook in the spring. In another tributary, closer to head of tide, there was no fall migration of large parr but a normal smolt migration in the spring. Saunders and Bailey (1980) suggest that fall movement of large parr is an adaptation in headwater stocks, placing potential smolts in the lower reaches of the river where they react to increased day length and rising water temperatures the following spring and undergo smoltification in time to move the remaining distance to the sea during the brief period when such entry is appropriate. If such behavior were inherent in former Connecticut River headwater stocks, as seems likely, this trait should be incorporated in stocks destined for nursery areas in that river.

Another large New England river which was once a major salmon producer, but for many years has had no salmon, is the Merrimack, with its tributaries in New Hampshire and mouth in Massachusetts (Stolte 1981). A major restoration program for the Merrimack River is in progress, using stock primarily from the Penobscot, a river of similar characteristics in Maine. The Penobscot lost all its salmon stocks by about 1958. Recently, pollution and obstructions have been overcome sufficiently that salmon can again use the river. Early attempts to recolonize the Penobscot were with salmon of Miramichi parentage (A. L. Meister personal communication). Plantings of locally reared smolts of Miramichi parentage in the Penobscot, Narraguagus, and Machias rivers were notably unsuccessful, giving few adult returns, most as grilse rather than larger salmon which were the typical salmon in these rivers. A major effort has been underway since 1967 to establish a self-sustaining Penobscot run. It was decided to stop using Miramichi fish and to use residual stocks from the Narraguagus and Machias. This project has produced a hatchery-assisted run of mainly early-run, 2-sea-year salmon. It is interesting that the donor streams had been previously stocked with Penobscot salmon and may, thereby, have served as refugia for a Penobscot stock or stocks which were absent from the Penobscot for some years. Recent runs of over 1000 adult salmon have been maintained through annual smolt plantings made as far upriver as possible so as to ensure that adults return to these sites which are suitable as nursery and rearing areas. Although there has been some spawning in the Penobscot tributaries (A. L. Meister personal communication), the run is still dependent on hatchery-reared smolts. While the run is mainly early (June−July), it does not have the early component (March−April) of the original one. Perhaps only limited components of the original Penobscot run were preserved in the Narraguagus and Machias refugia. A final note of interest with the Penobscot restoration is that several years' stocking of Miramichi fish did not alter the seasonal pattern of return or the age and size at maturity in the Narraguagus and Machias rivers. Moreover, Møller's (1970) gene frequencies for a transferrin allele were distinctive for these two rivers and widely divergent from any of his Miramichi samples.

The Saint John River system is the largest in New Brunswick and once produced a wide assortment of salmon types which supported large commercial and angling fisheries (Fig. 4). The combination of overexploitation, hydroelectric dams, and pollution has resulted in a great reduction in the number of fish in the once productive headwaters and the probable loss of many stocks (Elson et al. 1973; Dominy 1973; Ruggles and Watt 1975). The first major dam built on

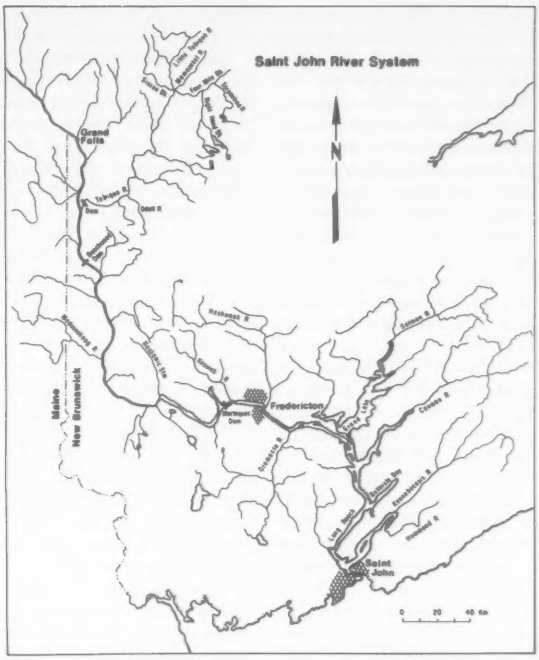

FIG. 4. Saint John River system showing principal tributaries accessible to salmon and locations of hydroelectric power dams.

the Tobique tributary at its mouth has an effective fishway that allows upstream movement of adults. Nevertheless, the run gradually diminished, possibly as a result of smolt loss through destruction in the turbines, smolt delay in the head pond, or further dam construction. The second dam, Beechwood, was built on the mainstem in the mid 1950s. It has a mechanical fish hoist. The run to the Tobique was further reduced as a result of smolt loss in the turbines and delay in the head pond. When the Mactaquac Dam was finished in 1966, it was considered that natural production in the headwaters would cease to be adequate if it continued at all. Accordingly, no fishway was built and a large hatchery (Mactaquac) with a production capacity of ~250 000 smolts was built to compensate for lost natural production. Mactaquac Dam has no fishway but a fish collection facility from which salmon are taken as hatchery broodstock and for trucking upriver to support an angling fishery and to allow natural production. Natural production has continued and the annual count of adult salmon (2452−27 765) at Mactaquac Dam has had a preponderance of naturally produced fish over those resulting from Mactaquac hatchery smolt releases since 1969.

The Tobique River is over 340 km long, has a number of tributaries with excellent spawning and rearing ground, and undoubtedly had a number of salmon stocks. Although the runs of adults were much reduced as a result of the hydroelectric dams, especially during construction of Mactaquac Dam, some of these stocks may have persisted. However, one important stock, the Serpentine, has been lost. Huntsman (1933) described these fish as bright but immature individuals which appeared in November in the Saint John Estuary. These fish apparently overwintered in the lower Saint John and made their way to the Serpentine where they supported an angling fishery early the following spring. Like some stocks of steelhead trout (Smith 1960), the Serpentine fish spent a year in the river, after returning from the sea, before spawning. The special migratory behavior of the Serpentine stock was unique among known stocks in New England and the Maritime Provinces. The Vistula, a long river in Poland, has or had a run similar to that in the Serpentine (Zarnecki 1963).

The strain of salmon being released from Mactaquac Hatchery probably has genetic material from a number of former or extant stocks in the upper Saint John. Although the Mactaquac spawners are multi-sea-year fish, the progeny produce at least as many grilse as multi-sea-year salmon. This observation is in contrast with the conclusion of Elson (1973) that age at first spawning is heritable with grilse parents producing mainly grilse offspring and 2-sea-year parents producing mainly 2-sea-year progeny. Two-year-old smolts from Mactaquac Hatchery usually give a preponderance of grilse when released in the Saint John, but fewer than 1% matured as grilse when reared in net pens in the Bay of Fundy (Sutterlin et al. 1981a). This is an example of genotypic−environmental interaction which may be further influenced by the mixed genetic background of the Mactaquac Hatchery strain.

The Miramichi is the largest salmon-producing system in eastern Canada. A ban on commercial salmon fishing was

begun in Miramichi Bay and estuary in 1972 because of very low runs in and before 1971. Data on the strength of various runs in the system are collected through angling catches and at a commercial-type monitoring trap net in the estuary. Annual parr census data are collected on a number of nursery areas by electrofishing. Counting fences were operated on various tributaries between 1950 and 1966 to estimate smolt production and spawning escapement. Miramichi runs were generally depressed following the start of forest spraying to control the spruce budworm plague (1950s), particularly in the early phase of the program when DDT was used at high concentrations (Elson 1967; Elson et al. 1973). In the early 1960s, during operation of a base metal mine on a tributary of the N.W. Miramichi (Fig. 3), the late run was much reduced and the early run delayed in reaching the headwaters (Saunders and Sprague 1967).

The Margaree River in Cape Breton, N.S. was formerly an excellent salmon producer having both early and late runs, each probably representing more than one stock. Both runs have decreased markedly during the past 20 years. The more valuable early run is barely surviving, probably because of heavy exploitation by the angling fishery (L. Marshall personal communication). Another possible cause of the reduced numbers of salmon is bacterial kidney disease (BKD) which is a serious problem in the Margaree Hatchery on a tributary of the river. Recent attempts to provide fish for summer angling were made by planting hatchery-reared, BKD-free smolts of Rocky Brook parentage, an early-run stream in the Miramichi system. This planting resulted in an estimated 6% return of early- run grilse in 1979 and substantial numbers of 2-sea-year adults in 1980.

Acid precipitation appears to have eliminated the stocks of salmon in 8 to 10 rivers in southwestern Nova Scotia; other rivers in Nova Scotia have pH values close to the lower acceptable value (Gourlay 1980). As the life stages most vulnerable to low pH are alevins and fry (Daye and Garside 1977), recruitment failure probably occurred during years while adults were still entering the rivers. This area of Nova Scotia is not only in the path of the prevailing wind drift from the northeastern United States, but it is also an area of acid waters because of the predominant granitic rock and extensive bogs. Other parts of the salmon-producing area of northern New England and the Maritime Provinces are threatened by acidification. The prospect of increased use of coal as an energy source in the northeastern United States increases the threat. Studies have begun to monitor pH changes in lakes and streams and possible effects on biotic communities. Some areas of predominantly granite bedrock are more susceptible to change in pH than are limestone areas which have greater buffering capacity in their soils.

Salmon Management in Recognition of Stocks

Salmon management in Atlantic Canada is complex; there are both commercial and angling fisheries, and, in recent years, a food fishery by Native peoples (Indian and Inuit) pursuing aboriginal claims to resources. Recognition of conflicts arising among user groups stimulated an extensive review of socioeconomic and biological aspects of the resource. One of the primary considerations arising from the *Atlantic Salmon Review* and the ensuing enhancement policy is allocation of the resource among the many users with priority given to conservation of stocks (Ritter et al. 1980).

The problem in attempts to regulate fisheries by stocks is that most commercial fisheries are situated in feeding areas or on major migration routes, a natural development as these are the places where fisheries would be most profitable. Although the policy for allocation of the salmon resource among commercial fishermen, anglers, and native people gives priority to conservation of stocks, the difficulty of pursuing this policy is in identification of stocks away from their spawning areas. In studies of the West Greenland fishery there are many references to stocks (Lear and Payne 1975; Payne 1973; Payne et al. 1976; Reddin and Burfitt 1979). Reddin and Burfitt report "... fish from a particular continent and fish from a particular stock tend to be grouped in certain areas at certain times at West Greenland so that more fish of a particular stock or stocks are concentrated in one area than another." This suggestion is based on the changing distributions in time and space of fish of North American origin.

The West Greenland fishery is based on salmon from North America and Europe (Parrish 1973) with little knowledge of stock identity beyond that provided by tags applied to smolts in their countries of origin. Gene frequency surveys through electrophoretic studies (Payne 1973; Payne et al. 1976), discriminant function analysis of growth patterns on scales (Lear and Sandeman 1974), and incidence of specific parasite infestation (Nyman and Pippy 1972; Pippy 1980) have been used as bases for assessing North American and European contributions to the Greenland fishery, but such information reveals little about individual stocks. Tagging studies give some indication of contributions from various rivers to the Greenland fishery (Saunders 1969; Elson 1970; May 1971; Peet and Pratt 1972; Turner 1972), but this method is costly and unwieldy. Reddin and Burfitt (1979) report that the proportion of North American salmon near Greenland fluctuates yearly, that North American salmon are in greater proportion in the Labrador Sea than at West Greenland, and that North American salmon are concentrated in greater proportion in the Labrador Sea during the spring than in autumn. Although this information does not constitute a basis for harvesting by stocks, it is invaluable as a means of assessing general abundance of North American salmon feeding near West Greenland.

Huntsman (1939) argued that salmon do not undergo directed movements or migrations but rather move in a random fashion, most staying within the influence of their home rivers. He said, "I have failed to find evidence that net fishing in the open sea or on an open coast has ever seriously reduced the stock of salmon, and I believe it fairly certain that such fishing would become quite unprofitable before there was serious reduction." During the same symposium, Menzies (1939) suggested, on the basis of tagging studies in Scotland and Norway, that there must be a feeding ground for European salmon at some indeterminate distance to the west of Norway and Great Britain. He suggested, further, that discovery of the major salmon feeding ground or grounds would endanger the species. Menzies was correct on both accounts; a fishery developed in West Greenland in the 1960s and its mixed stock nature complicates salmon management on both sides of the Atlantic. Huntsman (1972) continued to argue that salmon do not undergo migrations and that individuals reaching such

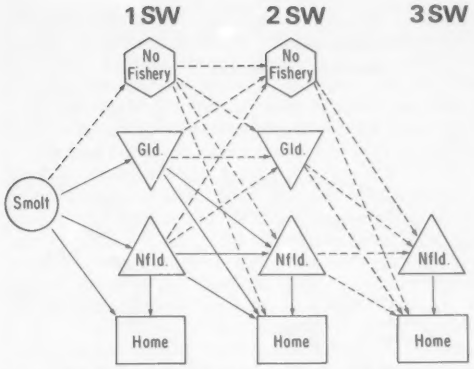

FIG. 5. Diagram illustrating variety of possible marine life patterns and their relationship to various fisheries. GLD = West Greenland, Nfld. = Newfoundland commercial fishery, Home = the area or river of origin of particular fish. Solid lines represent postulations based on tagging studies. Dotted lines represent postulations considered likely (from Prelim. Rep. of the Working Group on the Interception of Mainland Salmon in Newfoundland (Anon. 1980)).

distant places as Greenland were lost, and their capture there would have no serious effect on home fisheries. There is abundant evidence that the presence of salmon near Greenland and in other places distant from their home rivers represents true migration (May 1973) and that such open sea fisheries do pose a threat to commercial and angling fisheries and reproduction in home waters.

On the basis of smolt production, tagged smolts subsequently captured in Greenland and in home waters, commercial landings, and resulting recruitment in Miramichi waters, Paloheimo and Elson (1974) concluded that Miramichi stocks of salmon suffered marked reductions owing to the Greenland fishery during the late 1960s and early 1970s. Most of the Greenland catch is of potential two- and three-sea-winter salmon, roughly three-quarters of which are female (Parrish 1973). Paloheimo and Elson (1974) considered this loss of two-sea-winter spawners as a major cause of all-time low commercial catches and recruitment of young in the Miramichi during the late 1960s. They suggest that their findings for the Miramichi, which is responsible for about 60% of New Brunswick landings, represent Canadian Maritime rivers in general. Salmon which mature as grilse are not taken in Greenland waters; these fish feed closer to their continents of origin. Therefore, stocks which are comprised largely or entirely of grilse contribute little or nothing to the Greenland fishery. Examples are fish from Big Salmon River, N.B. (Jessop 1976), and Western Arm Brook, Nfld. (Chadwick et al. 1978). Ruggles and Ritter (1980) report that all the rivers for which they present smolt tagging and recapture data and which produce multi-sea-winter salmon make some contribution to the West Greenland fishery. However, recaptures of tagged Saint John River salmon in Greenland are proportionately fewer than those from the Miramichi River (Ruggles and Ritter 1980). This finding may be owing to tagged Saint John fish being captured mainly in a Greenland area that is less heavily fished than another area where most Miramichi fish are taken (Reddin and Burfitt 1979). These observations suggest that migratory patterns differ spatially and temporally among stocks.

A working group of biologists was formed in 1975 to study the commercial salmon fishery near Newfoundland–Labrador with the aim of developing proposals for change in the salmon fishery which would minimize the interception of salmon originating in the Maritime Provinces and Quebec with the least interference to harvest of those originating in Newfoundland–Labrador. The average annual catch in the Newfoundland–Labrador commercial salmon fishery during 1969–75 was 1.68 million kg, with estimated minimum contributions of 11 and 13.6% by stocks from the Maritime Provinces and Quebec, respectively (Anon. 1980). Models of the fishery were based mainly on recapture data for tags applied to smolts between 1968 and 1974 (Saunders 1969; Elson 1970; Peet and Pratt 1972; Turner 1972, 1975; Tétreault and Carter 1972; May and Lear 1971). These data showed that stocks of Maritimes–Quebec origin were distributed unevenly on both temporal and spatial bases in the commercial fishing areas around Newfoundland. Relatively few fish of mainland origin were taken in some parts of Newfoundland (along the west coast of the island) while in others from 6 to 51% of the catch was of mainland fish.

There is evidence for stock separation as shown by recaptures of tagged mainland-origin fish near Newfoundland. There is no en masse migration of mainland stocks through the Newfoundland commercial fishery. Some groups of salmon appear to be moving clockwise while others move counterclockwise around the island. There is preliminary evidence (D. G. Reddin personal communication) from late winter tagging of feeding salmon along the southern edge of the Grand Bank that some stocks may bypass the Newfoundland fishery on their way from feeding grounds to mainland rivers. Our understanding of the interception problem is complicated by the fact that the salmon in the waters around Newfoundland during a given season are a great mixture, some maturing and returning to home waters for spawning, and others actively feeding and not destined to mature for another year or more (Fig. 5).

Among the various options developed to reduce capture of salmon of Maritimes–Quebec origin in the Newfoundland–Labrador fishery, some would favor Maritime stocks more than those from Quebec and vice versa. Some stocks of Quebec origin could be subject to mixed stock fisheries in New Brunswick on their way to Quebec. Six possible regulatory approaches were considered as means of reducing interception in Newfoundland of salmon originating in the Maritimes and Quebec (Table 2). The approach calling for seasonal or flexible adjustment of fishing period was pursued in detail. Seven options were developed around times of opening and closing of the various fishing areas in Newfoundland. These considered estimated gains in number and weight of fish to the Maritimes and Quebec against losses to the present Newfoundland commercial fishery and gains to Newfoundland angling fisheries.

A first attempt to reduce interception of Maritimes–Quebec salmon in Newfoundland was the closure in 1972 of the Port-aux-Basques drift-net fishery which Belding and Préfontaine (1938) showed (Fig. 6) was based to a large extent on salmon returning to Maritime and Quebec rivers. A shore-based fishery was allowed to continue there. The catch has

TABLE 2. Possible regulatory approaches for solving the problem of interception of Atlantic salmon of mainland origin in the Newfoundland commercial fishery. Appeared as Table I in Preliminary Report of the Working Group on the Interception of Mainland Salmon in Newfoundland (Anon. 1980).

1. Stop Newfoundland fishery.

2. Do nothing.

3. A. Seasonal adjustment of fishing period:
   a) delay opening;
   b) early closure;
   c) shorter fishing week;
   d) moving time closure;
   e) fixed time closure.

   B. Flexible adjustment of fishing period:
   a) delay opening;
   b) early closure;
   c) shorter fishing week;
   d) moving time closure;
   e) fixed time closure.

4. Effort (by area):
   a) number of fishermen;
   b) fathomage limitation per berth;
   c) limitation of number of berths;
   d) mesh size limitation;
   e) fishing methods (offshore nets?);
   f) fishing berth location (estuarial fishery?);
   g) number of boats licensed.

5. Quota:
   a) total;
   b) by area
   c) by licence.

6. Key area restrictions

remained quite high owing to increased effort by the shore-based fishery and probably to increased by-catches in herring and mackerel nets. The major commercial salmon fisheries in the Maritimes and Quebec were also closed in 1972 because of alarming reductions in salmon catches. These closures were in the waters off the three major salmon-producing rivers, the Miramichi, Saint John, and Restigouche and the Gaspé region of Quebec. Salmon abundance in the large river systems and in other Maritime and Quebec rivers has recovered somewhat in recent years but not to the extent hoped for. This partial failure has been blamed on the continuing and possibly increasing fishery around Newfoundland together with by-catches of salmon in non-salmon fishing gear throughout Atlantic Canada, growing native food fisheries, increased angling harvests, and poaching. It has been suggested that some spawning populations of salmon are quite small (Møller 1970); adults of such stocks would be especially vulnerable to poaching and angling in their spawning areas.

The mixed stock fisheries off the Miramichi, Saint John, and Restigouche rivers are relatively less complicated and more easily managed than those in Greenland and Newfoundland; there are fewer stocks involved in each case. However, the major drift-net fishery off the Miramichi took salmon on their way to other New Brunswick and Quebec rivers (Belding and Préfontaine 1938) as well as those of

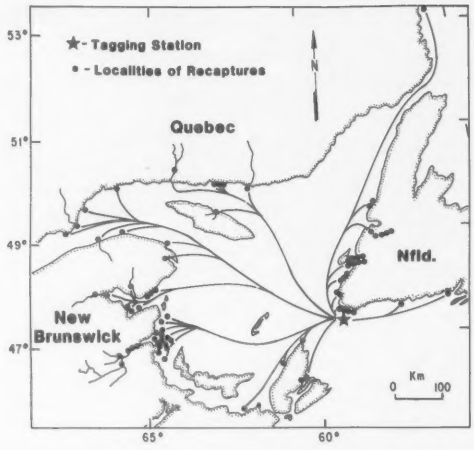

FIG. 6. Distribution of recaptured salmon tagged at Port-aux-Basques, Newfoundland in 1937 (from Belding and Préfontaine (1938)).

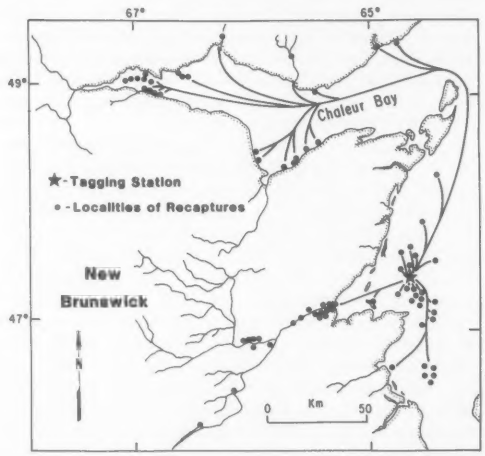

FIG. 7. Distribution of recaptured salmon tagged during the Miramichi drift-net fishery in 1937 (from Belding and Préfontaine (1939)).

Miramichi origin (Fig. 7). In view of the diversity of stocks in each of the major rivers, commercial fisheries close to them or in their estuaries exploited the runs largely without consideration of stocks. Commercial fishing seasons before the 1972 closure were mostly early, and this timing put great pressure on early-run stocks. However, it is not known to what extent late-run stocks were available to local fisheries even though they did not enter rivers until later in the season, usually after closure of commercial fisheries. The establishment of commercial fishing seasons, like selections for their location, depends more on fish abundance and quality than on

stock management considerations. The dangers to individual stocks in a commercial fishery in the estuary or lower reaches of a large river are obvious. Small stocks are liable to be fished below survival levels. Some stocks may be underexploited, leading to overcrowding on spawning beds and excessive seeding of nursery areas (Elson and Tuomi 1975).

The need for a greater consciousness of stocks in management of commercial and angling fisheries in respect to the Miramichi, Restigouche, Saint John, and Margaree rivers is shown in a recent Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) Advisory Document by the statement "... the implications of the harvest of a portion of these salmon stocks in the West Greenland, Newfoundland and Nova Scotia fisheries could not be fully evaluated." The year-to-year changes in the composition of the Greenland fishery should be monitored on a continuing basis with greater use of the discriminant function analysis of scale-growth patterns, not only as a basis for identifying continent of origin, but also for estimating contributions from major river systems or areas where genetic similarity and/or environmental conditions in nursery areas result in recognizable unique scale patterns. This technique together with smolt tagging should be used to provide more data for models leading to the best management strategy for allocation of Canadian salmon stocks. The excellent output from the Working Group should be continued and the most promising options tested.

We still lack a complete description and inventory of existing stocks. Surveillance of stocks in small rivers should be established. Small stocks in large river systems pose the greatest problem; these are most easily damaged and their declines least noticed. Electrophoretic studies of protein variation (Møller 1970; Allendorf and Utter 1979; Ståhl 1980), together with discriminant function analysis of adaptive variation in body morphology and behavior (Riddell and Leggett 1981; Riddell et al. 1981) will be useful in the separation and definition of salmon stocks. Riddell et al. (1981) point out that, as knowledge of variability among genetic units expands, it will rapidly become impractical to manage each recognizable genetic unit. They suggest that research efforts be directed to the definition of functional management units based on stepped clines and/or adaptive life history parameters.

Impact of Introducing Hatchery Fish in Streams

Salmon management in the Maritime Provinces and Maine has included numerous plantings of hatchery-reared juvenile salmon of various stages in all the major rivers and in many lesser ones (Møller 1970). In many cases, these plantings involved interchange of stocks to produce runs of salmon with different traits than usually found in the recipient river. Many attempts have been made to establish runs in barren rivers. Some of these attempts have been successful, but the results have seldom been evaluated with respect to contribution of the planted fish in comparison with strays from other rivers. Møller (1970) suggests that widespread stocking with hatchery fish, often progeny of relatively few parents and likely to have less genetic diversity than their parents, has not resulted in the breakdown of isolating mechanisms and genetic homogeneity. However, Møller concludes that interchange of stocks may have affected the gene frequencies of the original populations and he advises that interchange of stocks between different populations be avoided. He cautions, further, that if hatchery planting is to be done, the breeding population should contain as many spawners as possible to maintain an ample gene pool, and that parent stock should originate from the locality where the young are to be planted to assure a gene pool adapted to the local environment.

Some geneticists question, on theoretical grounds, whether or not hatchery-reared salmon are capable of reproducing in nature and of producing offspring sufficiently well adapted to new environments to establish self-sustaining populations. Runs of Atlantic salmon have resulted from smolt plantings, but it is difficult to prove that self-sustaining runs resulted from hatchery-reared fish rather than from strays from nearby rivers or naturally produced salmon already in the recipient stream. One such self-sustaining run of Atlantic salmon resulting from hatchery-reared juveniles is in the LaHave River, N.S. (Gray 1974). The LaHave salmon run has increased greatly during the 1970s as a result of building a fishway around the impassable falls together with regular stocking of hatchery-reared juveniles. Wild broodstock were collected from the LaHave and an adjacent river, the Medway (Gray and Cameron 1980). The mouth of the Medway is only 25 km from that of the LaHave and its headwaters are adjacent to those of the LaHave. There were few LaHave spawners so mainly Medway fish were used. By the mid 1970s there was a large population of naturally produced parr which must have come from adult returns from hatchery-reared parr and smolts, since observations of ascending adults through the fishway indicated there were too few wild spawners to have produced the observed parr population (R. W. Gray personal communication). An interesting footnote to the successful LaHave project is that there are some limestone soils in the catchment area and the river is likely to maintain a suitable pH whereas the nearby Medway has a lower pH and is likely to be lost as a salmon producer (Gourlay 1980).

Another self-sustaining run of salmon has been developed in the Big Salmon River, N.B. This river was without a run for many years when a dam blocked entry from the sea. The river was subsequently stocked with salmon and reputedly by brown trout × Atlantic salmon hybrids. Although Beland (1979) found no evidence that there has been introgression of brown trout genes into the present population, the fish in the Big Salmon River do resemble sea-run brown trout in certain respects. They have limited migration at sea (Jessop 1976), most of them mature initially as grilse, and they have a high incidence of multiple spawning (Ducharme 1969). In these respects, Big Salmon River fish are quite different from many of the salmon from the nearby Saint John River but are much like those found in several other short rivers entering the upper Bay of Fundy. Big Salmon River fish have chromosome numbers characteristic of Atlantic salmon, not of brown trout (F. L. Roberts personal communication). It is possible that the present run in the Big Salmon River was developed by strays from other Bay of Fundy rivers.

A major Atlantic salmon enhancement program is being planned for Atlantic Canada. The plan is to increase the production of salmon by several means: recover habitat that has been taken out of production through pollution or impassable barriers; make formerly inaccessible rivers and parts of rivers available for colonization; establish runs in barren rivers; increase production of existing salmon-producing rivers

through planting of hatchery-reared juveniles; produce runs of salmon through sea ranching (release of hatchery smolts) for commercial harvest or for angling; and produce salmon for market through intensive aquaculture.

Could such a program result in the destruction of salmon stock identity and lead to the production of domesticated salmon dependent on hatcheries for their continued existence? Clearly, there is not time to locate and identify all the salmon stocks before an enhancement program should be started. Some stocks may be damaged or destroyed as a result of extensive planting of hatchery fish. A strong risk to continuity of certain self-sustaining salmon stocks by introducing hatchery-reared juveniles must be accepted, but it can be minimized by applying existing biological knowledge. It is possible to produce runs of returning salmon by planting hatchery-reared juveniles at various stages. It is not known to what extent genetic structure of existing stocks would be changed. Møller (1970) says that possible genetic damage to existing stocks, and uncertainty as to whether an introduced stock influences gene frequency of the resulting mixture might be determined by introducing fish with known gene frequency which differs greatly from that in the recipient river, i.e. using genetic markers. A series of streams could be designated for experimental planting with hatchery smolts identified with internally readable microtags (Jefferts et al. 1963) and genetically marked with known gene frequency combinations. Returning adults would be selectively allowed to enter test streams with and without existing salmon populations. Resulting progeny in a barren stream would show that the introduced fish had spawned successfully. These progeny should be studied through another generation while continuing smolt plantings and controlling further entry of adult fish. Adults returning to a stream with an existing population would be selectively allowed entrance to see if adults resulting from hatchery-reared and naturally produced smolts interbreed and to what extent gene frequencies change in the subsequent generation.

A large potential exists for producing salmon through aquaculture, either cage rearing or sea ranching. This production of domesticated salmon need not threaten naturally produced stocks. Such production could help satisfy market demand and thereby reduce pressure on wild stocks. Cage rearing involves the hatchery production of smolts which are reared to market size in floating cages in suitable marine locations in eastern Canada where winter temperature does not reach the lethal level. This form of aquaculture is well developed in Norway where production in recent years has exceeded that of commercially harvested wild salmon (Sutterlin and Merrill 1978). Genetics research has played an important part in the development of the salmonid aquaculture industry in Norway (Gjedrem 1976a). Wild stocks have been screened for desirable production traits (Gunnes 1980), and a "gene bank" has been established to safeguard certain wild stocks which are threatened.

Sea ranching is another aquaculture strategy which will probably be used as part of a salmon enhancement program. Hatchery-reared smolts are released into a stream which they leave to spend a year or more in the sea and to which they return as adults (Saunders 1977). Recent experiments have shown that sea ranching need not be done from a river but that salmon can be made to "imprint" while being held in a seawater enclosure to which they return after 1 or more years at sea (Sutterlin et al. 1981b). This strategy makes it possible to produce a new run of salmon away from salmon-producing rivers and to minimize capture of wild fish along with sea-ranched ones. However, it is necessary to consider the effects of straying of sea-ranched salmon into streams supporting self-sustaining stocks. It must be recognized that salmon aquaculture is quite apart from maintaining genetic diversity and continuity of self-sustaining wild stocks. Aquaculture for intensive rearing and sea ranching involves selective breeding for production traits; this selection results in reduced genetic diversity and domestication.

In the 20 years since Professor Dymond predicted the demise of Atlantic salmon as a self-sustaining species, there has been further loss of spawning populations. Menzies' predictions concerning the existence of a major feeding area in the North Atlantic and the possible impact of its discovery have both been fulfilled. However, a developing high seas fishery off Greenland was curtailed and a reduced annual quota was established for a continuing nearshore fishery. Existing methods of stock identification offer promise of our being able to recognize and manage some stocks, or assemblages of stocks, in the Greenland and Newfoundland fisheries. There was a decline in the total catch of salmon in the Maritimes and Quebec during the early 1970s and steps were taken to rebuild runs by temporarily reducing commercial harvest. There appear to be effective means of reducing interception in Newfoundland of salmon originating in the Maritimes and Quebec. A new threat looms from long-range transport of atmospheric pollutants, i.e. acid precipitation. A number of Scandinavian stocks have been lost to acidification and some Canadian rivers have been affected. However, not all areas are susceptible to acidification and many rivers will continue to support salmon stocks.

Canada's planned enhancement program can help to increase numbers of salmon in the several ways suggested. A major concern is that high dependence on hatchery production and possible swamping of wild stocks with semidomesticated salmon will harm self-sustaining stocks. We have a good understanding of the genetic and environmental dynamics of stocks, but we have not learned how to put this knowledge to use. We must move cautiously to prevent the major effort to enhance the Atlantic salmon resource from putting further pressure on the species. We should proceed with the aspect of the enhancement program calling for extensive release of hatchery-reared salmon but on a narrow front at first so that incremental research results can refine applications in management to those that are least detrimental. I agree with Professor Dymond's prophesy that Canadian Atlantic salmon stocks are threatened and that more will be lost, but I believe that we have the scientific basis and management capabilities for keeping much of the quality and genetic variability in the remaining salmon resource.

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Biological Criteria for Definition of Species and Distinct Intraspecific Populations of Anadromous Salmonids Under the U.S. Endangered Species Act of 1973[1]

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UTTER, F. M. 1981. Biological criteria for definition of species and distinct intraspecific populations of anadromous salmonids under the U.S. Endangered Species Act of 1973. Can. J. Fish. Aquat. Sci. 38: 1626–1635.

The validity of most recognized species of salmonids under the biological species concept is supported by evidence from diverse sources. However, the specific status of a number of recently diverged populations remains uncertain. In the United States, it is particularly important to consider the possibility of unrecognized reproductively isolated populations for protection under the U.S. Endangered Species Act of 1973 (ESA).

Innate life history differences among species as well as numerous uncertainties within species preclude the use of a generalized model based on homing as the sole or primary means of defining discrete population segments of anadromous salmonid species. A process involving successive samplings, analyses, and syntheses of data from populations of a particular area is suggested. A major requirement of this process is reliable genetic data. The capability for the detection of allelic proteins by electrophoretic methods has provided a major tool for identifying and measuring genetic differences among populations and species. These data are necessary, but often insufficient for identifying most population segments and must be complemented by other biological and life history data as well as by historical and geological information. Provisional classifications of threatened or endangered populations on the basis of incomplete data may be necessary in many instances, but final classifications should depend on complete sets of data.

Transplanted and hatchery populations complicate the identification and management of anadromous salmonid populations under the ESA. Some evidence is cited that indicates a potential or actual adverse genetic effect of hatchery or transplanted fish on some native populations, and current studies designed to measure such effects are mentioned. The technical and economical feasibility for measuring these effects suggest that such measurements should be a requisite for new or extended transplantation and hatchery operations.

Further data are needed to determine whether or not threatened or endangered species and populations can be artificially perpetuated and still retain the capability to adapt to wild environments upon reintroduction to native habitats. This capability apparently exists in some domesticated strains of rainbow trout (*Salmo gairdneri*). However, large differences exist in the intrinsic levels of genetic variation between most domesticated populations of rainbow trout and many threatened or endangered natural populations of salmonids.

Key words: criteria, intraspecific, anadromous salmonid populations, genetic data

UTTER, F. M. 1981. Biological criteria for definition of species and distinct intraspecific populations of anadromous salmonids under the U.S. Endangered Species Act of 1973. Can. J. Fish. Aquat. Sci. 38: 1626–1635.

La validité de la plupart des espèces reconnues de salmonidés dans le concept de l'espèce biologique s'appuie sur des données provenant de plusieurs sources. Cependant, un grand nombre de populations qui ont récemment divergé ont un statut spécifique encore incertain. Il est particulièrement important aux États-Unis d'étudier la possibilité de l'existence de populations sexuellement isolées et non reconnues. Ceci dans le but de les protéger sous l'empire de la Loi américaine de 1973 sur les espèces en danger (ESA = *Endangered Species Act of 1973*).

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À cause de différences interspécifiques innées dans le cycle biologique ainsi que bien des incertitudes intraspécifiques, on ne peut utiliser un modèle généralisé fondé sur le homing comme seul ou principal moyen de définir des segments distincts d'une population de salmonidés anadromes. Nous suggérons un processus comportant des échantillonnages successifs, des analyses et des synthèses de données recueillies sur des populations d'une région particulière. Ce processus doit tout d'abord reposer sur des données génétiques fiables. Un outil important dans l'identification et la mesure de différences génétiques au sein de populations et d'espèces est la possibilité de détecter les protéines alléliques par des méthodes électrophorétiques. Bien que nécessaires, ces données sont souvent insuffisantes pour identifier la plupart des segments d'une population, et il faut les compléter avec d'autres données, tant biologiques qu'historiques et géologiques. Dans bien des cas, il faudra établir des classifications provisoires d'espèces en danger ou menacées en se fondant sur des données incomplètes. Les classifications définitives devront toutefois dépendre de séries complètes de données.

L'identification et la gestion des populations de salmonidés anadromes sous l'empire de la ESA se complique par suite de populations transplantées ou provenant de piscicultures. Nous citons quelques cas d'un effet génétique adverse, potentiel ou réel, de ces poissons sur certaines populations indigènes. Nous mentionnons également des études en cours portant sur la mesure de ces effets. Puisque la chose est techniquement et économiquement faisable, tout programme nouveau ou élargi de transplantation ou d'élevage devrait comporter la mesure de ces effets.

Il faudra davantage de données afin de déterminer si l'on peut ou non propager artificiellement des espèces et des populations menacées ou en danger et qu'en même temps elles puissent s'adapter à des milieux sauvages quand elles sont réintroduites dans des habitats naturels. Certaines lignées de truites arc-en-ciel (*Salmo gairdneri*) domestiquées semblent posséder cette aptitude. Il existe cependant de grandes différences dans les niveaux intrinsèques de variation génétique entre la plupart des populations domestiquées de truites arc-en-ciel et plusieurs populations naturelles de salmonidés menacées ou en danger d'extermination.

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THE rationale for the U.S. Endangered Species Act of 1973 (ESA) as amended in 1978 can be paraphrased as follows: Every animal species of the United States — as well as isolated populations within some species — represent unique and irreplaceable groups of organisms containing actual or potential ecological, scientific, historical, recreational, esthetic, and educational value; all such groups warrant responsible management and, where necessary, protection. The assessment of the current status of such groups, leading to possible protective or remedial actions, requires a sound biological basis for the identification of both species and populations.

This paper is a response to this requirement in conjunction with a mandate of the National Marine Fisheries Service, NOAA, to assess the status of certain U.S. stocks of anadromous salmonids relative to the ESA. Its objectives are (1) to state reliable criteria that can be applied to defining both species of anadromous salmonids as well as discrete populations within species, and (2) to consider some of the confounding aspects of transplantations and hatchery management on possible ESA actions. The complexities and uncertainties of defining and identifying species and populations are examined primarily in the context of salmonid literature. Syntheses are made from these data to outline the general requirements for defining species and distinct population segments for the implementation of such definitions in accordance with the ESA.

Definition and Characterization of Species

The reality of the taxonomic level called "species" is accepted among most biologists within the framework of the definition: "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups" (Mayr 1970). The recognized species of salmonids are generally consistent with this definition. Each of the five species of Pacific salmon (*Oncorhynchus*) that are indigenous to North America frequently exist sympatrically with one or more congeneric species (Aro and Shepard 1967; Atkinson et al. 1967). Yet these species remain readily identifiable throughout their ranges. The coastal forms of sea-run rainbow trout (steelhead) (*Salmo gairdneri*) and cutthroat trout (*S. clarki*) trout likewise occur sympatrically, although they are fertile in laboratory crosses (J. Mighell, NMFS, personal communication), they do not significantly interbreed in nature.

The five species of Pacific salmon and the two trout species mentioned above have each evolved and diverged from common ancestors for periods probably exceeding 10^5 years (Neave 1958). One may safely assume that their ancestral forms very likely resembled one another much more than do the forms existing today.

Sympatric Populations

Assuming that the processes leading to speciation (e.g. see Stebbins 1971) are more or less continual, it is reasonable to suggest that populations in the process of incipient speciation currently exist in salmonids. Evidence for noninterbreeding of conspecific salmonid populations that coexist in the same area would support the contention that these populations are genet-

TABLE 1. Allelic frequencies of sympatric demes of brown trout in Lake Bunnersjoarna, Sweden. Allocation to deme is based on phenotype of the LDH-1 locus (from Ryman et al. 1979). χ^2 = chi-square values for differences between demes (2 × 2 contingency tests). (Significance: *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$).

Locus (allele)	Deme I, LDH-1 (100/100)	Deme II, LDH-1 (240/240)	χ^2
AGP-2 (100)	0.976	1.000	4.82*
CPK-1 (100)	0.562	0.293	26.04***
EST-2 (100)	0.967	0.886	3.37
LDH-5 (100)	0.872	1.000	12.63***
MDH-4 (100)	0.571	1.000	51.08***
SDH-1 (100)	0.891	1.000	10.58***
SOD (100)	0.989	1.000	0.01

ically isolated from one another and are in the early stages of processes leading to complete reproductive isolation (i.e. speciation). Such evidence exists from investigations of salmonid populations and some of it will be briefly reviewed below.

Innate tactic responses leading newly emerged salmonid fry either upstream or downstream to lakes serving as nursery areas have been demonstrated in sockeye salmon (*O. nerka*) from diverse geographic regions (Raleigh 1971; Brannon 1972). These responses were altered through individual crosses involving both inlet and outlet parents indicating the inadaptive nature of natural crosses between inlet and outlet populations of a given drainage. This inadaptiveness infers the genetic isolation of such populations sharing an otherwise common environment.

Two morphologically distinct groups of Bonneville whitefish (*Prosopium spilonotus*) were found to coexist in Bear Lake on the Utah–Idaho border (White 1974). Each form was distinct with regard to growth, and to age and size at maturity. It was recommended that each group be given tentative recognition as different species.

Direct genetic evidence for noninterbreeding of two brown trout (*S. trutta*) populations coexisting in a small Swedish lake has been reported (Allendorf et al. 1976; Ryman et al. 1979). These groups (identified on the basis of distinct biochemical genetic profiles, see Table 1) had different growth rates and spawning areas. It was postulated that one group was a relict population that had been isolated within a glacial refuge about 125 000 years ago whereas the second represented a more widespread group of brown trout that recently reinvaded the area. Although it may be argued whether or not these two groups are sufficiently reproductively isolated to warrant their classification as distinct species, they are clearly diverging towards such a distinction. Similar sympatric populations of Arctic char (*Salvelinus alpinus*) have also been reported (Nyman 1972).

Direct evidence for sympatric populations of sockeye salmon has been found in sockeye salmon populations of the Lake Washington drainage near Seattle, Washington. Genetic differences of proteins have identified a population of nonanadromous sockeye salmon in Issaquah Creek of the Lake Washington drainage that is distinctly different not only from other non-anadromous and anadromous sockeye salmon populations of this drainage but also from all sockeye salmon populations outside of this drainage that have been studied (Utter et al. 1980).

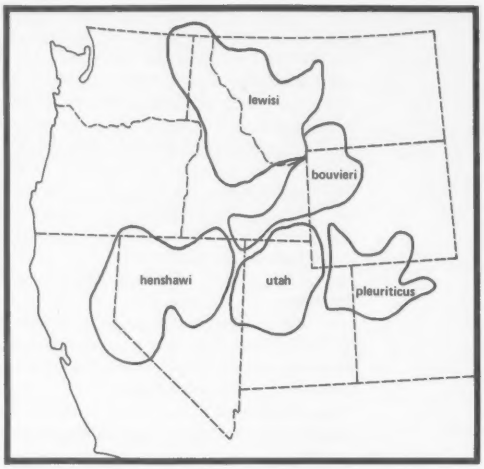

FIG. 1. Approximate distribution of inland subspecies of cutthroat trout (*Salmo clarki*). Adapted from Loudenslager and Gall 1980.

The above examples describe diverged and sympatric conspecific populations of salmonids that are in presumably early or intermediate phases of speciation. It is very likely that other, possibly numerous, similar instances exist among such species of salmonids in view of the recent and isolated efforts that have been made towards their detection.

ALLOPATRIC POPULATIONS

Another segment of the species question concerns nominally conspecific populations that are temporally or geographically isolated from other populations. These populations may be in various stages of incipient speciation, but their capabilities for maintaining genetic isolation under sympatric conditions cannot be assessed. The inland cutthroat trout complex represents a series of geographically isolated groups of populations (Fig. 1) where recent estimates of genetic distances demonstrate substantial genetic divergence among some of the groups suggesting incipient speciation (Loudenslager and Gall 1980). A detailed examination of the population structure of the coastal group (*S. clarki clarki*) over a limited geographic range (Campton 1981) indicated a strong tendency to maintain the integrity of local populations, further suggesting the possibility of isolates within this group that may be diverging towards speciation.

Pink salmon (*O. gorbuscha*) is the best known example of temporal isolation in salmonids. Their rigid 2-yr life cycle has led to two distinct gene pools throughout their species range (Fig. 2). Extensive geographic surveys of genetic variation have identified a greater similarity within a year-class, regardless of geographic origin, than between year-classes, even in the same streams (Aspinwall 1974; Johnson 1979; Donnelly et al. 1979). Even- and odd-year pink salmon have also evolved different intrinsic growth rates (Ricker et al. 1978),

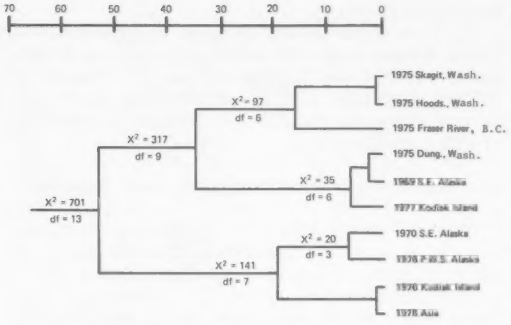

FIG. 2. Dendrogram of *AGP*, *PGM-1*, *MDH-3*, *4*, and *AAT-3* gene frequency clustering for pink salmon among the geographic regions sampled. The heterogeneity χ^2 for pooled samples is given at each statistically significant bifurcation (summed over all loci). From Johnson 1979.

distinct geographic distributions (Aro and Shepard 1967: Atkinson et al. 1967), and differential temporal and distributional spawning patterns having a heritable basis within individual drainages used alternately by both year-classes (Helle 1970; Taylor 1980). It is evident that the two year-classes are diverging towards ultimate speciation if their genetic isolation persists.

NOMINAL SPECIES

The phenotypic plasticity and diverse life history capabilities of many salmonids have historically confused the species picture in some instances. Thus, two phenotypically different groups having nonoverlapping geographic distributions and distinct life history patterns may be categorized as separate species and yet be sufficiently closely related to not warrant such a distinction.

The current taxonomic status of rainbow trout (*S. gairdneri*) and related population groups is a possible example of this situation. This group of populations comprises two recognized species (*S. gairdneri* and golden trout, *S. aguabonita*) plus a third population complex, the redband trout, that has been nominally elevated to species rank in much of the current literature (see Gold 1977). The taxonomic status of redband trout has been complicated by differing concepts of its scope (Bakke 1977; Behnke 1979) and by genetic evidence indicating that different populations having similar physiological adaptations have arisen from distinct lineages (Wishard et al. 1980).

Although it is beyond the scope of this report to make a detailed review of these groups of rainbow trout — like populations (see Behnke 1965; Gall et al. 1976; Gold 1977; Wilmot 1974; Wishard et al. 1980), it is pertinent to examine the genetic similarity [i.e. values between 0 and 1 averaging the level of detectable genetic similarity between two populations over all loci examined — usually greater than 20, (see Rogers 1972; Nei 1972)] among these generally recognized species groups in contrast with those among the subspecies of cutthroat trout. Loudenslager and Gall (1980) have reported an average genetic similarity (based on electrophoretic data from ~ 40 loci) of about 0.85 among three major interior subspecies of cutthroat; Campton (1981) has identified a similar divergence of the coastal subspecies from other cutthroat groups. However, the genetic similarity among the species complex of rainbow–golden–redband trout (based on data analogous to the cutthroat trout comparisons) is above 0.925 in all comparisons between populations (Allendorf and Utter 1974; R. Smith, Univ. Cal., Davis, CA, personal communication; Wishard et al. 1980). The purpose of making this contrast is not to debate the validity of the species rank in one group or the subspecies rank in the other (although such a debate on a detailed presentation and synthesis of the known facts of the matter is clearly in order), but to point out the pitfalls inherent in the necessarily arbitrary nature of species classification based primarily on morphological criteria, particularly at the early stages of divergence.

It is evident, then, that uncertainties do exist concerning species classification and identification among salmonids. Some of these uncertainties are important to consider with regard to the implementation of the ESA because of the converse possibilities of either considering two or more noninterbreeding groups to be a single panmictic unit or granting unwarranted separation to minimally diverged populations. These problems will next be considered at the within-species level.

Definition and Identification of Distinct Population Segments

The processes resulting in the formation of distinct intraspecies populations are the early phases of those ultimately leading to speciation, with the primary distinction being (by definition) the absence of reproductive isolation. The strong homing tendencies of anadromous salmonids make this group particularly susceptible to the formation of such populations. Given this common characteristic, it is tempting to formulate a generalized model for migratory salmonids in which a hierarchy of areas, major streams, and tributaries is used to define the basic population unit.

The model does provide a useful first approximation of reality. The regularity of the return of various species with regard to location and time has been well documented in the salmonid literature (reviewed in Ricker 1972). Examinations of comparative genetic attributes of these runs in different species (as methods have become available) have demonstrated that genetic similarity tends to increase directly with geographic proximity (Utter et al. 1974; May 1975; Kristiansson and McIntyre 1976; Grant 1977; Thorgaard 1977a; and Allendorf and Utter 1979).

The model has significant deficiencies, however, that preclude its use as the sole criterion for defining distinct population segments of anadromous salmonid species. It assumes a single continual radiation of population segments from an initial starting point and fails to consider geological or biological events that may result in discontinuities of such a predicted radiation. Thus, the model would predict that the greatest similarity would be within major drainages when considering proximal populations of the Columbia and Fraser Rivers just upstream and downstream from the Cascade Crest. However, morphological and biochemical evidence have independently shown just the opposite to be true (Behnke 1979;

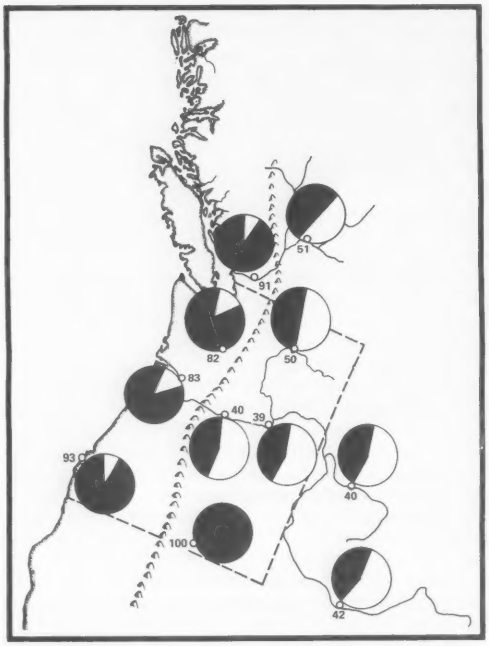

FIG. 3. Representative frequencies of the *LDH-4 (100)* allele (solid portion of circles) averaged from populations of rainbow trout-like fishes of the Pacific Northwest. Frequencies typify three population groups (a) west of the Cascade Crest, (b) east of the Cascade Crest in the Fraser and Columbia River drainages, and (c) in desiccated inland basins of southern Oregon. Data obtained from Allendorf 1975; Utter and Allendorf 1977; Milner et al. 1980; Wishard et al. 1980.

Allendorf 1975; Utter et al. 1980). The conclusion that the populations either east or west of the Cascade Crest have, respectively, the greatest similarity regardless of drainage is supported by knowledge of recent geological events that explains the adjacent location of diverged populations (Fig. 3). Geographic discontinuities of population units of coho and chinook salmon that deviate from the model have also been reported (Allendorf and Utter 1979).

A second deficiency of the model is the tacit assumption of a relatively uniform capability for radiation among the different anadromous species. Much evidence has accumulated to indicate that capabilities for radiation differ significantly among anadromous salmonids as a reflection of the evolution of distinct life history patterns (reviewed in Utter et al. 1980). In addition, transplantations[2] interfere with heritable patterns of homing precision (Ricker 1972) and further complicate innate differences among species in the formation of discrete population groupings.

The above discussion does not negate the application of a stream distance model, but places strict limits on its use. Generalizations cannot be made between species because of differing geographic ranges of interbreeding populations. Generalizations within species must consider the possibility of natural or man-made discontinuities.

DATA REQUIRED FOR IDENTIFYING POPULATION SEGMENTS

It is pertinent at this point to ask about the kinds of data that are required to best identify a distinct population segment as the model based on homing requires supplemental data to provide generally reliable information. An ideal set of data should have a purely genetic basis because data reflecting environmental variables could indicate homogeneity among genetically discrete populations occupying similar habitats and thus give misleading information. These ideal data should reflect the particulate nature of genetic variation at individual loci (i.e. Mendelian variation) to quantify genetic differences. The magnitude of measurable differences between any two populations should be a direct reflection of the total genetic variation that separates these groups. A sufficient sampling of variant loci would be needed to increase both the probability of finding genetic differences between populations and the accuracy of measurements estimating relationships among populations. Finally, these data should be attainable with reasonable efforts so that statistically meaningful sample sizes can be obtained.

The ability to define distinct population segments in salmonid species has been limited in the past through the absence of data fulfilling the above criteria. A review of morphological, physiological, and behavioral approaches used to examine the distribution of genetic variation within species of Pacific salmon (Ricker 1972) indicated: (1) much genetic variation existed among populations of Pacific salmon and (2) homing had a strong genetic basis and was the most definitive indicator of population structure. Nevertheless, the discreteness of the underlying genetic variation remained unknown and this precluded any quantification of purely genetic differences among populations. Homing has also been excluded as a primary criterion for population definition because of the limitations outlined above. The inability of these methods to provide generally reliable genetic definitions of population structures does not negate the overall value of these data which cumulatively add great wealth to understanding the biology of Pacific salmon and which occasionally (usually through a combination of distinct homing and timing) actually identify discrete population segments.

Studies of allelic variations of proteins (i.e. electrophoretically detected biochemical genetic data) have recently received increasing attention as a tool in fisheries research and management (reviewed in Utter et al. 1974; Allendorf and Utter 1979) and fulfill more of the idealized criteria outlined above for data required to identify discrete population segments than any other known method. The use of protein data has added a new dimension to the study and understanding of interspecific and intraspecific relationships of salmonids. Indeed, most of the recent advances in the understanding of such relationships are the direct result of interpretations of protein data.

[2]Intentional transplantations and introductions of stocks by man significantly compound the problem of population identification and discontinuity; the population units described here, unless specifically designated otherwise, are presumed to be a reflection of natural distributions, and the topic of introduced populations will be considered in a later section.

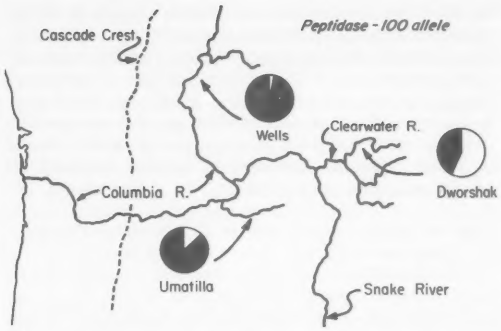

FIG. 4. Frequencies of the *Peptidase-1 (100)* allele (solid portion of circles) from three populations of the Columbia River drainage (from Utter and Allendorf 1977). Subsequent sampling has verified the high frequency of alternate allelic forms at the Dworshak Hatchery and the predominance of the *(100)* allele from all other collections of both the Snake and Columbia Rivers (Milner et al. 1980).

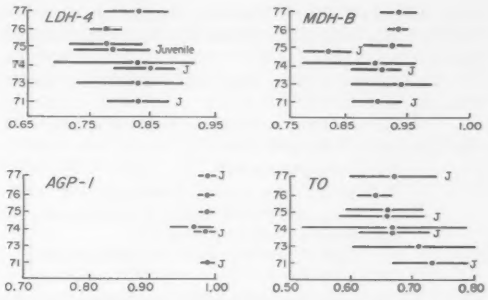

FIG. 5. Allelic frequencies and 95% confidence intervals at four loci for juvenile and adult steelhead trout from the Chambers Creek Hatchery (Washington State Department of Game) over a 7-yr interval (from Utter et al. 1980). The outlying in *MDH-B* of the 95% confidence interval of the 1975 juvenile collection beyond intervals of some other collections is attributed to sampling error under the 5% expectation for such an occurrence.

Although protein data are a valuable addition to the tools used to study the genetic structure of populations, they should not be regarded as a panacea. For instance, it may be properly concluded from consistently different frequencies of allelic variants in collections of fish from two different areas that a real genetic difference exists between the populations of these areas. However, the absence of variation among different collections taken within each area does not, in itself, justify concluding that the collections of that area were drawn from a single genetically homogeneous population.

The validity of this principle can be illustrated in two examples. Allendorf (1975) initially identified two major population groups of steelhead in the Columbia River where the upstream populations were not strongly separated within the upper Columbia River or Snake River branches. Subsequent data based on additional protein systems (Milner 1977) strongly separated steelhead of the Dworshak Hatchery (Snake River) from populations of the upper Columbia River (Fig. 4). The second example concerns the Yellowstone cutthroat trout (*S. clarki bouvieri*) for which biochemical genetic data from geographically distinct populations have revealed minimal allelic frequency differences (Loudenslager and Kitchin 1979). Nevertheless, populations within the subspecies have demonstrated a large diversity of physiological adaptations to widely different environments (Varley 1979) and innate differences of tactic responses have been observed in emergent fry from inlet and outlet streams in Yellowstone Lake (Raleigh and Chapman 1971). Thus, the absence of protein variation among populations did not preclude the existence of considerable genetic diversity.

It is important to consider whether or not the geographical distribution of protein variants strongly reflect environmental variation. Strong differential responses of allelic proteins to environmental variables could result in a single interbreeding population having different frequencies of protein variants in different environmental settings. If this were the case, other variables having a less discrete genetic basis (e.g. meristic counts) may be more appropriate markers for the actual genetic structure of the population. The consistency of allelic frequencies of protein variants in populations of anadromous salmonids has been recently examined throughout life cycles in single generations, between generations, and among overlapping year-classes. All comparisons demonstrated the temporal stability of allelic frequencies (Fig. 5) and justifies their use primarily as markers of variation among populations rather than among environments (Utter et al. 1980). An analogous situation exists in man, where relationships deduced by the distribution of protein variants approximates anthropological estimates of true relationships whereas a different set of relationships based on external morphological features is more a reflection of ancestral environments (Cavalli-Sforza 1971; Patterson 1978).

What then are appropriate data requirements for identifying discrete population segments within an anadromous salmonid species having established: (1) that a model based only on homing is inadequate by itself and (2) that sets of protein data are necessary but generally incomplete for adequate identification? The complexities of different situations preclude a simple generalized solution. Rather, each situation must be regarded as unique which, in fact, it is. However, a logical sequence of processes can be outlined which should lead to satisfactory results.

I) Accumulate background data on the region in question.

a) Examine the history of the species in this area using:

1) Transplantation records or reliable anecdotal information.

2) Records of population sizes, spawning times, and spawning locations past and present.

3) Documentation of man-induced changes in the environment.

4) Compilation of all available allelic frequency and meristic data and other data pertaining to genetic structure of populations.

5) Any studies pertaining to this species in or from this region that could contain valuable information.

b) Look into the geological record of the region for

clues suggesting former isolation in presently continuous drainages that may have resulted in a multiplicity of populations.

II) Collect data from a systematic sequence of samples from this area.

a) Initially sample at extreme ranges of the area using data from phase I for guidelines.

1) Collect protein data.

2) Measure other biological variables (e.g. meristic, timing, and growth data) that may provide clues suggesting reproductive isolation.

3) Measure physical and biological aspects of habitat differences.

b) Synthesize data from initial sampling to determine the next approximation towards identification of population structure of the region.

c) Repeat processes IIa and IIb on a successively finer scale.

III) Determine the structure and biological status of the populations of the area. Successive approximations based on preceding samplings, data collections, and syntheses lead ultimately to an answer based on a thoughtful and thorough analysis of the best available data.

The process is necessarily vague. Beyond the early stages of phase II there is no way to estimate realistically the amount of work (and hence the cost) involved in obtaining the ultimate answers because of the numerous uncertainties that vary with every situation; such is the nature of scientific inquiry. Nor is there any certainty as to what methods will provide the ultimate answers, particularly in instances where differences detected by protein data are minimal. Cytogenetic studies have complemented protein data in examining the genetic structure of steelhead populations (Thorgaard 1977a, b) although the amount of intraspecific variation is not nearly as extensive as protein variation and therefore may not be generally applicable. A promising process which examines enzymatically fragmented mitochondrial DNA (Avise et al. 1979) may also be acceptable when this process becomes further developed. Other procedures that detect some degree of genetic variation remain useful but lack the capability of precise genetic identification of distinct population units.

On the other hand, the three-phased format outlined above is flexible and applicable both to interspecific and intraspecific problems. Proper implementation in conjunction with the ESA promises a wealth of new insights into the structure of salmonid populations and the dynamics of speciation.

Finally, it is important to recognize that many situations may require remedial actions prior to a time frame that would permit the full implementation of this process. Provisional decisions based on incomplete data (i.e. phase I) may be necessary in such instances. Final decisions could then be based on subsequent revisions as additional data became available through the fulfillment of phases II and III.

Biological Implications of Transplanted and Hatchery Populations

The management of anadromous salmonids in the western United States during the last century has involved the development of hatcheries and the mass transplantation of fish stocks. These developments considerably complicate the applications of the ESA to the management of these populations. Some of these complexities are principally not biological and will not be examined here. For instance, the question of whether or not an artificial run that is self perpetuating (e.g. the sockeye salmon run in Cedar River near Seattle) should be protected under the ESA is pertinent, but beyond the scope of this paper. Questions pertaining to some of the biological complexities are examined below.

What is the Biological Impact of Transplanted or Hatchery-Adapted Populations on Indigenous Populations?

This question is a major concern in current salmonid management and its answers have a direct bearing on implementation of the ESA. There has been much conjecture concerning the possibility of negative effects on native populations of supplemental plantings of nonnative and hatchery fish. A major potential threat, over and above competition, predation, and disease communication, is interbreeding of introduced fish with native populations. Until recently, it has been difficult to measure directly these effects although Behnke (1979) has reported morphological evidence of interbreeding of introduced salmonids with native interior cutthroat trout populations, and the ultimate replacement of much of the native interior cutthroat trout populations with introduced or hybrid forms. A negative result of this introgression has been the apparent loss of the capability for large individual growth that formerly existed in some interior cutthroat populations. Some of this introgression has been confirmed and quantified with allelic frequency data based on differing characteristic protein patterns of native and introduced species (Allendorf and Phelps 1981). Conversely, other studies of rainbow trout populations have indicated no evidence of introgression into native populations in spite of extensive histories of hatchery plantings (Wishard et al. 1980).

Some data are accumulating on the genetic impact of hatchery plants on native populations. A long-term study by the Washington State Department of Game is in progress on the Kalama River to study the immediate and long-term interactions of hatchery-planted and indigenous steelhead trout populations. Hatchery fish are identifiable by a specially bred protein variant (i.e. genetically marked) so that the variant will be passed on to descendants and the actual genetic impact of these plants can be measured indefinitely beyond the first generation (Crawford et al. 1978, 1979). Reisenbichler and McIntyre (1977), also using genetically marked fish, identified genetic differences affecting growth and survival between hatchery and wild steelhead trout of the Deschutes River, Oregon, where performance of wild fish was best in stream environments and that of hatchery fish was best in pond environments. The Washington State Department of Fisheries has been engaged in a long-term commitment to study the genetic impact on naturally spawning fish of selected chum salmon enhancement projects since 1976 and has currently extended these efforts to other salmon species (Seeb and Wishard 1977; Wishard 1980). A study is in progress which will compare the genetic structures of steelhead trout populations of the Skagit River in Washington (Campton

1979) where heavy hatchery plantings have been made for many years, with the genetic structures determined from recently completed studies of tributaries of the Fraser River of British Columbia (Parkinson 1980) where management is based on native fish: these comparisons should provide valuable insights into the effects of hatchery management on population structures.

The above investigations are model studies for measuring the genetic impact of hatchery fish on native populations. More studies of this nature are clearly needed, particularly in situations where management involving large-scale transplantations and artificial propagation is just beginning (e.g. ocean ranching). It is now both technically feasible and economically realistic to quantify the genetic impact of transplanted and artificially propagated fish on native fish over time and space; it is irresponsible to ignore this capability.

Can Endangered Populations be Perpetuated by Artificial Propagation?

Behind this question lies a more penetrating question with regard to the ESA: does artificial propagation of endangered populations irrevocably alter those qualities that make a particular population worthy of protection under the ESA? The evidence is compelling that the process of "domestication" genetically alters the adaptive qualities of a population (e.g. see Reisenbichler and McIntyre 1977). However, a systematic examination has not been made to determine whether or not domesticated populations retain the capabilities to revert to the original wild state. If generally affirmative data are obtained, the primary focus can be on perpetuation of the population, regardless of changes in the habitat.

There is a great deal of evidence demonstrating the capability of domesticated rainbow trout to become established in diverse habitats (MacCrimmon 1971; Behnke 1965; VanVelson 1978). This evidence is consistent with the recent finding of high average heterozygosity within most domesticated strains of rainbow trout (Allendorf and Utter 1979; Busack et al. 1979) and suggests that many hatchery strains have retained a sufficient pool of genetic variation to adapt to a variety of natural habitats despite a century of domestication.

However, this possibility has not been adequately tested by controlled experimentation or systematic observation, and even if true, it would be dangerous to extrapolate to even closely related species (or subspecific taxa) where a data base is minimal or nonexistent. Recent observations have demonstrated that genetic variation is often lost in the process of establishing hatchery strains from wild populations of salmonids (Ryman and Stahl 1980; Allendorf and Phelps 1980); thus a representative sampling of the gene pool in question must be obtained in establishing a cultured population. It is also important to recognize that species or populations requiring protection under the ESA have most likely lost much genetic variation through severe reductions in population sizes and therefore probably have gene pools with significantly reduced levels of genetic variation relative to those of outbred rainbow trout populations. Such populations may therefore lack the genetic plasticity to adapt to conditions of culture or to subsequently readapt to natural environments. Conversely, the flexibility of artificial culture has not been considered to this point, and it is feasible to simulate natural conditions to a much greater extent than is commonly done in salmonid hatcheries. The possibility of perpetuating wild populations of salmonids by artificial propagation in conjunction with the ESA therefore cannot be generally resolved at this point; each situation will probably have to be separately considered following a thorough examination of its pertinent biological attributes.

Conclusions

1) A multitude of biological, geological, and historical variables in anadromous salmonids preclude any a priori criteria for adequately defining either species or discrete population segments within species in a given geographical area. The requirement of genetic data for adequate definition initially places severe limitations on most sets of data from a particular area because of the absence or incompleteness of such data from most situations where action under the ESA may be considered. A general sequence of events leading to the collection of suitable data for describing the structure of breeding units of a species in a particular area includes first accumulating available background data, then determining by successive approximations what data are missing and obtaining them, and finally, synthesizing the breeding structure of the area from the complete set of data. Although the uncertainties of this process preclude quick decisions in most instances, provisional determinations on the basis of limited data are possible in areas where prompt remedial action is warranted followed by final decisions when more complete data become available.

2) The understanding of the natural breeding structure of anadromous salmonid populations has been complicated in many areas by transplantations and hatchery management over a long period of time. The impact of these practices on natural populations is highly conjectural at this time and the limited available data vary greatly from case to case; it is important that future programs involving transplantations and hatchery management be designed to include the evaluation of their effects on native populations. The long cultural and transplantation history to rainbow trout indicates that many strains are capable of successfully establishing self-perpetuating populations in diverse habitats. This capability should not be generalized to threatened or endangered populations of anadromous salmonids which very likely lack the genetic plasticity of most cultured rainbow trout populations; however, specialized cultural practices may permit reestablishment of some threatened or endangered populations in restored habitats.

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Changes in the Average Size and Average Age of Pacific Salmon[1]

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RICKER, W. E. 1981. Changes in the average size and average age of Pacific salmon. Can. J. Fish. Aquat. Sci. 38: 1636–1656.

Of the five species of Pacific salmon in British Columbia, chinook salmon (*Oncorhynchus tshawytscha*) and coho salmon (*O. kisutch*) are harvested during their growing seasons, while pink salmon (*O. gorbuscha*), chum salmon (*O. keta*), and sockeye salmon (*O. nerka*) are taken only after practically all of their growth is completed. The size of the fish caught, of all species, has decreased, but to different degrees and over different time periods, and for the most part this results from a size decrease in the population. These decreases do not exhibit significant correlations with available ocean temperature or salinity series, except that for sockeye lower temperature is associated with *larger* size. Chinook salmon have decreased greatly in both size and age since the 1920s, most importantly because nonmaturing individuals are taken by the troll fishery; hence individuals that mature at older ages are harvested more intensively, which decreases the percentage of older ones available both directly and cumulatively because the spawners include an excess of younger fish. Other species have decreased in size principally since 1950, when the change to payment by the pound rather than by the piece made it profitable for the gill-netters to harvest more of the larger fish. Cohos and pinks exhibit the greatest decreases, these being almost entirely a cumulative genetic effect caused by commercial trolls and gill nets removing fish of larger than average size. However, cohos reared in the Strait of Georgia have not decreased in size, possibly because sport trolling has different selection characteristics or because of the increase in the hatchery-reared component of the catch. The mean size of chum and sockeye salmon caught has changed much less than that of the other species. Chums have the additional peculiarity that gill nets tend to take *smaller* individuals than seines do and that their mean age has increased, at least between 1957 and 1972. That overall mean size has nevertheless decreased somewhat may be related to the fact that younger-maturing individuals grow much faster than older-maturing ones; hence excess removal of the smaller younger fish tends to depress growth rate. Among sockeye the decrease in size has apparently been retarded by an increase in growth rate related to the gradual cooling of the ocean since 1940. However, selection has had two important effects: an increase in the percentage of age-3 "jacks" in some stocks, these being little harvested, and an increase in the *difference* in size between sockeye having three and four ocean growing seasons, respectively.

Key words: Pacific salmon, age changes, size changes, fishery, environment, selection, heritability

RICKER, W. E. 1981. Changes in the average size and average age of Pacific salmon. Can. J. Fish. Aquat. Sci. 38: 1636–1656.

Des cinq espèces de saumons du Pacifique en Colombie-Britannique, les saumons chinook (*Oncorhynchus tshawytscha*) et coho (*O. kisutch*) sont récoltés durant leur saison de croissance, alors que les saumons rose (*O. gorbuscha*), keta (*O. keta*) et nerka (*O. nerka*) ne sont capturés qu'une fois leur croissance pratiquement terminée. Chez toutes les espèces, la taille des poissons capturés a diminué, mais à des degrés et sur des périodes différents. Ceci résulte en grande partie d'une diminution de taille dans la population. Il n'y a pas de corrélations significatives entre ces diminutions et les séries disponibles de températures et de salinités dans l'océan, sauf que pour le saumon nerka, une plus basse température est associée à une *plus grande* taille. La taille aussi bien que l'âge des saumons chinook a diminué considérablement depuis les années 1920, surtout parce que la pêche aux lignes traînantes capture des sujets qui ne sont pas en voie de maturation. Comme résultat, les individus qui mûrissent à des âges plus avancés sont exploités plus intensivement. Ceci, à son tour, a pour

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effet de réduire le pourcentage de vieux poissons disponibles, tant directement que cumulativement, puisque les reproducteurs comprennent un surplus de jeunes poissons. La taille des autres espèces a diminué surtout depuis 1950, alors qu'on adoptait un mode de paiement à la livre plutôt qu'à la pièce; il était plus profitable pour les pêcheurs aux filets maillants de récolter davantage de grands poissons. Les plus fortes diminutions se sont produites chez le saumon coho et le saumon rose. Il s'agit d'un effet presque entièrement génétique provenant du fait que les lignes traînantes et les filets maillants commerciaux capturent des poissons de taille supérieure à la moyenne. Cependant, les saumons coho élevés dans le détroit de Géorgie n'ont pas diminué de taille, possiblement parce que la pêche sportive à la ligne traînante exerce une sélection différente, ou par suite de l'augmentation des poissons d'élevage dans les prises. La taille moyenne des saumons keta et nerka capturés a changé beaucoup moins que celle des autres espèces. Une autre particularité des saumons keta est que les filets maillants ont tendance à capturer des sujets plus petits que ceux capturés à la senne, et que leur âge moyen a augmenté, du moins entre 1957 et 1972. Le fait que la taille moyenne en général a quand même un peu diminué peut être lié à un taux de croissance plus rapide d'individus mûrissant à un plus jeune âge que ceux murissant à un âge plus avancé, de sorte que l'enlèvement du surplus de jeunes poissons tend à ralentir le taux de croissance. Chez le saumon nerka, une augmentation du taux de croissance liée au refroidissement graduel de l'océan depuis 1940 a, semble-t-il, ralenti la diminution de taille. Cependant, la sélection eut deux effets importants : une augmentation du pourcentage des « jacks » de 3 ans dans certains stocks, peu exploités, et une augmentation de la *différence* de taille entre saumons nerka ayant respectivement trois et quatre saisons de croissance en mer.

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Background

It is well-known that domestic and experimental animals can be changed by selection in a multitude of ways: in the direction of faster or slower growth, larger or smaller final size, more or less body hair, scales or feathers, resistance to disease, and so on. Fish are no exception to this rule; among other things, they have been successfully selected for rapid growth, early maturity, and greater egg production. This plasticity has led biologists to speculate about possible effects of unintentional selection by fisheries on stocks of fish in the wild.

A common feature of most fisheries, both sport and commercial, is that they harvest the faster-growing members of a stock somewhat more heavily than those of slower growth because they are the first to become large enough to be caught. Thus the breeding stock tends to contain a greater proportion of slow-growing individuals than when natural conditions prevail, so a gradual change in the heritable component of growth rate seems likely, making for slower growth cumulatively. However it has proved very difficult to obtain reliable information on this effect for most fish stocks. Generally speaking, the average size of the fish caught today is less than it was in (say) 1900, but this is mainly because they are younger. If we compare growth rates today with those of samples taken early in the century, the picture is complicated by the possibility that reduced abundance has permitted faster individual growth. Thus any hereditary effects of man's selection on the size of the fish in wild stocks have for the most part remained unknown, although this does not necessarily mean that they have been unimportant.

Another possible effect of fishing on wild fish stocks is to decrease the average size at first maturity. If a fish matures before it is large enough to be vulnerable to fishing, its expectation of contributing to future generations will be greater than that of a sibling of the same size that does not mature until a year later. The result can be a gradual decrease in mean size of first maturity.

The five American species of Pacific salmon offer favorable opportunities for studying changes both in rate of growth and in age of maturity. Over the past decades several colleagues and I have addressed these questions. Reports on changes in size or age of individual species have appeared in papers by Milne (1957), Godfrey (1958, 1959a, b), Wickett (1965, 1973), Ricker (1972), and Bilton (1973). Recently a more comprehensive review has been made for each species in a series of Technical Reports (Ricker et al. 1978; Ricker 1980a, 1980b, 1981; Ricker and Wickett 1981). These contain the extensive tabular data that are the necessary basis for conclusions concerning the extent and the causes of past and current changes. The present paper is a summary.

All Pacific salmon have an important characteristic that simplifies the study of changes in growth rate and age of maturity: each fish matures only once and then dies. Also, for each species there is a rather small number of possible ages of maturity, varying from 1 to 6 or 7. Another favorable circumstance is that in British Columbia three of the species are harvested only after their growth has been completed, or practically so. Table 1 summarizes these features.

Fishery Regions

The Technical Reports cited above made some reference to changes in size or age of salmon in Alaska, Oregon, and California, but this paper deals only with British Columbia. Commercial statistics in British Columbia are reported by numerous areas and three large districts (Fig. 1). The lake and river systems that contain major salmon runs, particularly of sockeye salmon (*Oncorhynchus nerka*), are the Nass in area 3, the Skeena in area 4, the Owikeno in area 9, and the Fraser

TABLE 1. Ages of maturity and times of harvest of Pacific salmon (*Oncorhynchus*) in British Columbia.

Species	Principal ages of maturity	Principal time of harvest
Pink (*O. gorbuscha*)	Age 2 only	Near the end of the 2nd year of life
Chum (*O. keta*)	Age 3, 4, or 5	Near the end of the 3rd, 4th, or 5th year
Sockeye (*O. nerka*)	Age 3, 4, 5, or 6	Near the end of the 4th, 5th, or 6th year
Coho (*O. kisutch*)	Age 2 or 3	Near the end of the 2nd year of life and throughout the 3rd year
Chinook (*O. tshawytscha*)	Age 2, 3, 4, 5, or 6	Throughout the 2nd to final year of life

in area 29. However, salmon bound for these rivers are taken, to varying extents, in other areas; this is especially true of the Fraser, whose salmon are also subjected to a major fishery in United States waters.

AGE OF SALMON

Pacific salmon go to sea during the year of hatch or during the 1st or 2nd (rarely the 3rd) subsequent year. All systems of designating age have disadvantages. The one used here specifies the number of *completed* seasons of freshwater and of ocean growth, using the convention that all growth in the year the fish go to sea is called "ocean" growth even though part of it may be made in freshwater (true of coho salmon (*O. kisutch*) sockeye, and especially chinook salmon (*O. tshawytscha*)). Thus a salmon that went to sea during its 3rd growing season and is currently in its 3rd year of ocean growth is designated as 2.2 or 2/2. The term "age" means the number of growing seasons completed, with the convention that a growing season ends at the end of a calendar year (except as noted below). "Ocean age" is the number of growing seasons that have been completed in the ocean. However, at time of spawning salmon are considered to have just completed their final growing season and their age designations increase by 1. For example, most cohos caught in ocean or river fisheries are of age 2 and ocean age 1 (age 1.1); the spawners, however, are of age 3 and ocean age 2 (age 1.2).

GEAR SELECTIVITY

Salmon caught in gill nets are subject to various types of selection, depending on the size of mesh used. We must distinguish between target species and incidentally caught species. For a target species size of mesh, etc., will be adjusted to obtain a maximum catch of that species. Prior to the Second World War this usually meant the largest number of fish because most salmon were sold by the piece, irrespective of weight. "Red spring" chinooks were the only consistent exception. Typical prices about 1935 were 5 cents for pink salmon (*O. gorbuscha*) and chum salmon (*O. keta*), 10 cents for cohos, and 25 cents for sockeye. With this schedule, sockeye were obviously a preferred target species wherever they occurred in any numbers.

In 1945 a change was made, and soon all species were sold by weight. It then became advantageous to use nets whose maximum catching power was for somewhat larger than average specimens of the target species because in this way poundage and value would be maximized. The required change in mesh size was not great, and because the mean size of the fish varied a good deal from year to year, there was no *sudden* change in the mesh used. Also, the introduction of nylon nets during the 1950s probably gave the selectivity curve of a given mesh a broader dome than formerly. Thus buying by the pound has introduced a tendency for mean weight of target species taken by gill net to be larger than the average weight in the run as a whole. In catch statistics this appears as a larger average size among gillnetted fish than among seined fish.

The mode of selection of nontarget species, taken incidentally by other gill net fisheries, varies according to their size. For example, chinook salmon taken incidentally in a sockeye gill net fishery are much smaller than their average length in the run of that time. Similarly, pink salmon taken incidentally in a gill net fishery for any other salmon are strongly selected for large size in the catch and resulting small size on the spawning grounds. Under these circumstances the difference in mean size between those caught and those that escape can be quite large, larger than differences within the target species. Significant selective effects are possible even when no great proportion of a species is taken in this fashion. Notice that when, for example, pinks and sockeye occur together, sockeye will be the target species even if they are considerably less abundant than pinks because of the latter's smaller size and smaller value per pound.

It is a matter of observation that commercial troll fisheries have been selective for large size among coho, pink, and sockeye salmon; for chinooks there is no good information. Up to about 1965 the pinks and sockeye taken by troll were mainly incidental catches in fisheries for chinooks and cohos, but since then they have increasingly become target species at times and places where they are abundant. For pinks, this has meant that the troll-caught fish are not as much larger than seine-caught pinks as they were formerly.

The troll fisheries for chinooks and cohos are also selective in another way. They take the fish while they are actively feeding and growing, which means that individuals that first reach legal, acceptable, or catchable size in a given year are exploited over a longer period than those that grow more slowly. This effect may be somewhat diluted by mortality among rejected individuals, the so-called "shaker" loss (Ricker 1976).

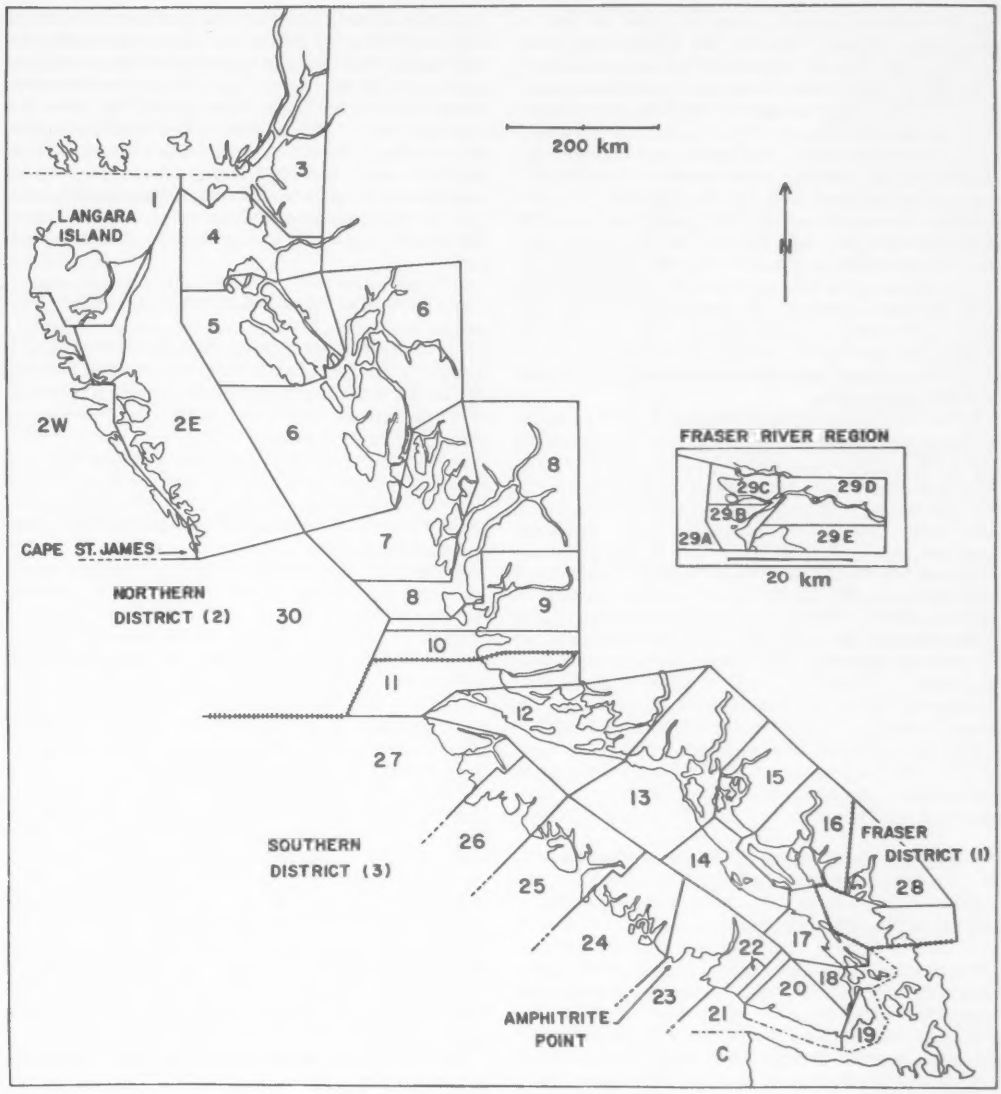

FIG. 1. Statistical areas and districts in British Columbia.

In the case of chinooks, there is also much greater utilization of individuals that mature late because they are exposed to the fishery for additional growth years.

Selection by gill nets and trolls has been detected by comparing size in their catches with that in seines operating in the same area. The nature of seine gear suggests that it should tend to catch salmon independently of their size because the meshes used are small enough to retain all maturing individuals except coho of ocean age 1 and some of the sockeye of ocean age 2 (jacks). This of course is not a complete guarantee of nonselectivity because salmon of one size may be more active than another in escaping the closing seine or jumping over the cork line. In the absence of factual data, all that can be said is that seines seem likely to be much less selective than gill nets; if selective at all, it would presumably be the larger and stronger fish that are best able to escape being caught.

HERITABILITY

Selection by the fishery refers to fish that die without reach-

ing the spawning grounds. From the point of view of reproduction, however, "selected" fish are those that escape the fishery and take part in producing the next generation.

Heritability of a quantitative character is determined mainly by the additive genetic variance in a stock and the variability of its environment (Falconer 1976). Greater genetic variance means greater heritability, and greater environmental variability means less heritability. For quantitative treatment four concepts are employed. The *selection differential* (S) is the difference between the average size of parents and that of the stock from which they were selected. The *response to selection* (R) is the difference in size between the unselected stock and the progeny of the selected parents, when both are reared under the same conditions. The *intensity of selection* (i) is equal to S/σ, where σ^2 is the phenotypic variance of the stock in respect to the character selected. *Heritability* (h^2) can be estimated in various ways, but estimates here are all made from the quotient R/S.

In this work the response to selection is taken to be the observed rate of change in size per generation, as averaged over a series of years, i.e. size in the filial generation compared with what it was in the parental generation *before selection*. The two generations, of course, are reared 2 to several years apart, hence not necessarily "under the same conditions" as specified above. In fact, if a unidirectional trend in environmental conditions exists, or can even be imagined, then it is always possible that a "response" measured as above is partly or wholly an environmental effect. Arguing against this is the fact that the one known environmental trend is, with one exception, not significantly correlated with salmon sizes, as described in the Effects of Changes in the Environment section, and that exception runs contrary to the observed change, i.e. it would make the fish larger instead of smaller. In any event we need to calculate apparent heritabilities wherever possible and see if they are of the order of size expected from comparison with observations on other fishes and other animals.

Sources and Reliability of Information on Size and Age

Sizes from Commercial Catches

The most continuous and consistent sources of information about sizes of salmon in British Columbia are the annual commercial catch statistics reported by the Canadian Department of Fisheries. These begin in 1951 and at time of writing are available through 1979; however, many of the computations here have been made for 1951 through 1975 only. The statistics report the number of salmon caught by each type of gear separately, by weeks and "statistical months"; weight is given for each gear by statistical months only. A statistical month consists of 5 calendar weeks for January, April, July, and October, and 4 calendar weeks for other months. Thus the position of a statistical month varies from year to year, the maximum difference between median dates being 7 d.

The published statistics are compiled from sales slips made out for each primary delivery of salmon from fisherman to buyer. These slips include both the number and weight of the fish caught. Weight is always obtained directly, for the fish are paid for by the pound. For landings of up to a few dozen, or perhaps 100 or so, the fish are counted individually. For large landings it is clear that an average weight is sometimes used to compute the numbers. This average may be based on a sample from the landing, or from a general "feel" about how large the fish look, or how large the fish have been in other recent landings. This of course introduces the possibility of error, but much indirect evidence shows that it is not important for our purpose. This comes from four sources.

1) Variations in size from year to year are similar between adjacent areas and between catches taken by the three types of gear.

2) Trends in size with time differ greatly between species; within each species different parts of the coast exhibit different rates of decrease. In the case of pink salmon, the odd-year rate of decrease differs markedly from that for even years. If decrease in size were an artifact of changes in procedure or in carefulness, it should affect all species taken by a given gear more or less equally, and there should be more consistency in the other matters mentioned.

3) In the case of chum and sockeye salmon there have been sampling programs that provide an indication of mean length (and, for sockeye, weight) over a considerable period of years. These data, independently obtained, exhibit year to year fluctuations in size similar to those from the sales slips.

4) There are important differences in the tabulated sizes of salmon taken by different kinds of fishing gear in a given area. However, if these differences were artificial they would presumably be consistent between species. In fact, however, among sockeye, pink, and coho salmon gillnetted fish tend to be larger than seined fish from the same area, whereas among chums the seined fish are usually the larger. This difference can be explained on the basis of mesh sizes used in the gill nets, but there could scarcely be a human bias that operates in opposite directions for different species.

It is of course possible, indeed inevitable, that there have been accidental errors in the original records, in copying, or in the computations of mean weights. I can only say that reasonable care, repetition, and cross-checking have been used at all stages. Tables have been inspected for unusually high or low mean weights, and most of the few that were found could be corrected by consulting the original records. The remainder were omitted if completely unreasonable but otherwise were allowed to stand. The surviving errors of these and other types are evidently too few and too small to spoil the consistent picture of variation and change in mean size.

Statistics of sport fisheries are not used in this paper; the best summary is by Argue et al. (1977).

Sampling Programs

Starting in 1914, there has been a series of annual samples of sockeye salmon taken from the major runs by Fishery Officers. Begun by C. H. Gilbert and continued by W. A. and Lucy Clemens and D. R. Foskett, the series was summarized and continued up to 1972 by Bilton et al. (1967a, and later reports). The lengths and weights are tabulated for each sex of each life-history type, as determined by scale reading.

Starting in 1957, H. T. Bilton and colleagues also sampled chum and pink salmon taken by nets and reported lengths for

each sex and (for chums) at each age. This series continued through 1972 (Bilton et al. 1965, 1966, 1967, 1967a, b, 1968; Jenkinson et al. 1969; Jenkinson and Bilton 1970, 1971, 1972, 1973).

For the Fraser River region there are additional chum samples by Palmer (1972), from both catch and escapement. The International Pacific Salmon Fisheries Commission lists the mean weight of the dominant life-history type of sockeye salmon in its Annual Reports. Other samples have been taken for short periods of time, sometimes in connection with tagging experiments. These have been summarized in the Technical Reports.

Effects of Changes in the Environment

Before ascribing any trends in size of salmon to selection, it was necessary to examine the possibility that they could be the result of trends in environmental conditions. The long-term trends in temperature of the surface layers of the northeastern part of the Pacific Ocean have been a gradual rise from the 1910s to about 1940, and a decline thereafter. Comparisons of temperature and salmon size are made in the Technical Reports. Here it is only necessary to state that correlations between size and temperature in individual years were sometimes positive, sometimes negative, and were usually nonsignificant. Where the sign of the correlation was right for explaining the time trends in size, and assuming it to be real, the rate of change in size computed from the regression on temperature was always much less than the observed change, in the case of pink, chum, and coho salmon. This was true even using GM regressions (Ricker 1973), which indicated much larger effects than did the ordinary regressions.

Sockeye, however, were exceptional in that since 1943 their size has exhibited a fairly consistent and strong negative correlation with ocean temperature at station P (50°N, 145°W), particularly the Fraser River fish. This was first reported by Killick and Clemens (1963). Although the negative correlation of size with observed temperature has since become numerically less because the two series have had the same declining trend, a negative correlation between *residuals* of size and of temperature (deviations from their respective regression lines) has continued and has even become numerically a little larger. The rate of decrease, based on the GM regression, is about 0.94 lb/°C (0.43 kg/°C). Combined with a decrease in temperature at station P of 0.0196°C/yr, this represents an increase in size of 0.0183 lb/yr (8.3 g/yr), or 0.44 lb (200 g) over the 24 yr from 1951 to 1975.

Comparisons have also been made between salmon sizes and ocean salinity. A tentative relationship for cohos was reported by Wickett (1973), but it later petered out. No other promising leads have been discovered.

Pink Salmon

Decrease in Size

Because of their uniform 2-yr life history, pink salmon size changes reflect rate of growth only; they are not complicated by changes in the proportion of different ages in the catch.

Pinks that mature in odd-numbered years tend to be larger than those maturing in even-numbered years, the mean difference being about 1.1 lb (500 g) (Fig. 2). Both lines decreased in size between 1951 and 1975 (Tables 2 and 3, Fig. 3). In spite of being smaller to start with, even-year pinks have decreased at a more rapid rate than odd-year pinks; for seine-caught fish the mean rate was 0.041 lb/yr (19 g/yr) in odd years and 0.071 lb/yr (32 g/yr) in even years. The actual decrease was from 5.5 to 4.3 lb (2.5 to 2.0 kg) in odd years and from 4.6 to 3.0 lb (2.1 to 1.4 kg) in even years, during 1951–75.

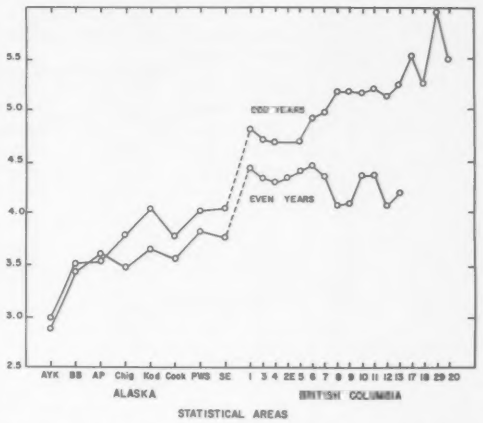

FIG. 2. Trends in the mean weight in pounds of pink salmon catches, arranged geographically from north and west to south and east. Figures for Alaska are for 1960–74 and include catches by all gears; those for British Columbia are for 1951–75 and represent gill net catches only.

Selection and Heritability

Seines and gill nets have been the gears usually used to catch pink salmon, and trolls have become important in recent years. Both gill nets and trolls catch pinks of larger mean size than seines do. Considering the seines to be nonselective, this has meant that larger pinks have been more heavily harvested than smaller ones, so that the spawning escapement has consisted of fish of less than average size each year. Estimates of this size difference (the selection differential), on the basis that 80% of the pink stock is harvested, have been compared with the observed decrease in size per generation (the response to selection, if all of the decrease is a result of selection). Their ratio is 0.22 for odd years and 0.30 for even years. These estimates of the heritability of size in pink salmon lie within the range of heritabilities of size that have been observed in other fishes and in domestic animals (Falconer 1976; Ricker et al. 1978).

There are three aspects of the decrease in size of pink salmon that would be very difficult or impossible to ascribe to environmental causes, but can readily be explained on the basis of selection by the fishery. (1) The even-year lines of (small) pinks have decreased in size more rapidly than the odd-year lines of (larger) fish. This will occur if the same nets are used in both odd and even years and if their maximum

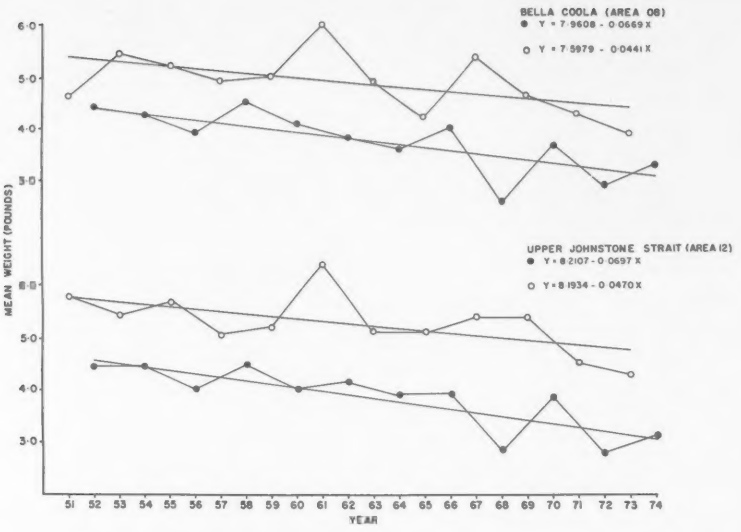

FIG. 3. Mean whole weights of net-caught pink salmon in areas 8 and 12, 1951–74. Y = weight in pounds; X = time in years, year 0 being 1900.

TABLE 2. Trends in mean round weight in pounds of pink salmon caught by three gears in odd-numbered years. N = number of years' data used; r = linear correlation coefficient; b = regression coefficient (lb/yr); 1951 and 1975 = computed sizes (lb) in the years indicated; change = computed change in size between 1951 and 1975 (1b). All means are weighted by the figures shown in the catch column, which are the total number of pinks caught by all gears during the odd-numbered years 1951–75, in units of 100 000 (*$P < 0.05$, **$P < 0.01$).

Region	Area	Catch	N	r	b	1951	1975	Change
				Gill net				
Northern	1	6	12	−0.047	−0.0028	4.85	4.78	−0.07
	3	65	13	−0.629*	−0.0439	5.24	4.19	−1.05
	4	96	13	−0.739**	−0.0477	5.25	4.10	−1.15
Hecate Strait	5	53	13	−0.694**	−0.0411	5.19	4.20	−0.99
	6	66	13	−0.515	−0.0294	5.26	4.55	−0.71
Central	7	45	13	−0.275	−0.0139	5.14	4.80	−0.34
	8	75	13	−0.200	−0.0110	5.32	5.06	−0.26
	9	9	13	−0.766**	−0.0437	5.71	4.65	−1.06
	10	3	13	−0.709**	−0.0277	5.49	4.82	−0.67
District 2 means					−0.0323	5.25	4.47	−0.78
Johnstone Strait, etc.	11	3	9	−0.627	−0.0419	5.70	4.70	−1.00
	12	261	13	−0.395	−0.0223	5.39	4.86	−0.53
	13	74	13	−0.368	−0.0223	5.50	4.97	−0.53
Georgia Strait	17	2	10	−0.417	−0.0302	5.89	5.17	−0.71
	18	2	7	−0.820*	−0.0725	6.12	4.38	−1.74
Fraser	29AB	56	13	−0.337	−0.0257	6.26	5.65	−0.61
Juan de Fuca	20	209	13	−0.350	−0.0182	5.71	5.27	−0.44
NW Vancouver I.	27	11	6	−0.108	−0.0023	4.70	4.60	−0.10
District 3 and 1 means					−0.0211	5.58	5.08	−0.50
Overall means					−0.0256	5.45	4.83	−0.62
Percentage change								−11.4%
				Seine				
Northern	1	6	9	−0.736*	−0.0900	6.07	3.91	−2.16
	3	65	13	−0.773**	−0.0762	5.44	3.62	−1.82
	4	96	11	−0.808**	−0.0886	5.75	3.61	−2.14

TABLE 2. (*Concluded*)

Region	Area	Catch	*N*	*r*	*b*	1951	1975	Change
Hecate Strait	2E	3	8	−0.285	−0.0196	5.02	4.55	−0.47
	5	53	13	−0.568*	−0.0496	5.02	3.83	−1.19
	6	66	13	−0.734**	−0.0567	5.06	3.71	−1.35
Central	7	45	13	−0.601*	−0.0444	4.91	3.84	−1.07
	8	75	13	−0.618*	−0.0487	5.22	4.05	−1.17
	9	9	9	−0.667*	−0.0744	5.70	3.91	−1.79
District 2 means					−0.0640	5.31	3.78	−1.53
Johnstone Strait, etc.	12	261	13	−0.502	−0.0342	5.63	4.80	−0.83
	13	74	13	−0.389	−0.0264	5.57	4.94	−0.63
Georgia Strait	17	2	9	−0.550	−0.0261	5.79	5.17	−0.62
	18	2	12	−0.177	−0.0092	5.62	5.40	−0.22
Juan de Fuca	20	209	13	−0.370	−0.0275	6.11	5.45	−0.66
District 3 means					−0.0305	5.81	5.07	−0.73
Overall means					−0.0450	5.59	4.51	−1.08
Percentage change								−19.3%
				Troll				
Northern	1	6	13	−0.590*	−0.0549	5.94	4.63	−1.31
	3	65	12	−0.608*	−0.0654	5.91	4.33	−1.58
	4	96	12	−0.683*	−0.0714	6.04	4.32	−1.72
Hecate Strait	2E	3	11	−0.367	−0.0524	5.58	4.32	−1.26
	5	53	10	−0.390	−0.0896	6.32	4.17	−2.15
	6	66	10	−0.640*	−0.1452	7.24	3.75	−3.49
Central	7	45	13	−0.715**	−0.0740	6.15	4.37	−1.78
	8	75	13	−0.757**	−0.0665	6.07	4.48	−1.59
	9	9	6	−0.843*	−0.1212	6.74	3.83	−2.91
	10	3	4	−0.912	−0.0787	6.26	4.37	−1.89
District 2 means					−0.0845	6.27	4.24	−2.03
Johnstone Strait, etc.	11	3	9	−0.462	−0.0906	7.07	4.99	−2.17
	12	261	13	−0.504	−0.0504	6.19	4.98	−1.21
	13	74	13	−0.449	−0.0401	5.95	4.99	−0.96
Georgia Strait	17	2	10	+0.144	+0.0144	5.52	5.87	+0.35
Juan de Fuca	20	209	13	−0.226	−0.0212	6.15	5.65	−0.50
West coast of	21	9	13	−0.436	−0.0299	6.14	5.43	−0.71
Vancouver I.	23	17	13	−0.477	−0.0440	6.29	5.29	−1.05
	24	12	13	−0.524	−0.0455	6.32	5.23	−1.09
	25	6	13	−0.474	−0.0435	6.19	5.14	−1.05
	26	5	13	−0.437	−0.0494	6.47	5.28	−1.19
	27	11	13	−0.569*	−0.0606	6.52	5.06	−1.46
District 3 means					−0.0386	6.16	5.24	−0.93
Overall means					−0.0574	6.21	4.83	−1.38
Percentage change								−22.2%

TABLE 3. Trends in mean round weight in pounds of pink salmon caught by three gears in even-numbered years. All means are weighted as the total number of pinks (in hundred thousands) caught by all gears during the even-numbered years 1952−74. Other symbols as in Table 2 (*$P < 0.05$, **$P < 0.01$).

Region	Area	Catch	*N*	*r*	*b*	1952	1974	Change
				Gill net				
Northern	1	60	12	−0.651*	−0.0485	4.97	3.91	−1.06
	3	72	12	−0.700*	−0.0427	4.80	3.87	−0.93
	4	85	12	−0.672*	−0.0426	4.77	3.84	−0.93
Hecate Strait	2E	47	11	−0.495	−0.0233	4.60	4.09	−0.51
	5	150	12	−0.752**	−0.0449	4.91	3.92	−0.99
	6	274	12	−0.828**	−0.0610	5.14	3.80	−1.34
Central	7	90	12	−0.679*	−0.0369	4.77	3.95	−0.82
	8	311	12	−0.824**	−0.0581	4.71	3.44	−1.27
	9	43	12	−0.828**	−0.0529	4.66	3.50	−1.16
	10	7	12	−0.726**	−0.0344	4.74	3.98	−0.76
District 2 means					−0.0510	4.86	3.74	−1.12

TABLE 3. (*Concluded*)

Region	Area	Catch	*N*	*r*	*b*	1952	1974	Change
Johnstone Strait, etc.	11	2	9	−0.665*	−0.0453	4.86	3.86	−1.00
	12	189	12	−0.759**	−0.0423	4.53	3.59	−0.94
	13	18	10	−0.084	−0.0108	4.31	4.07	−0.24
West coast of Vancouver I.	27	10	9	−0.019	−0.0009	4.07	4.05	−0.02
District 3 means					−0.0378	4.49	3.65	−0.84
Overall means					−0.0489	4.80	3.73	−1.08
Percentage change								−22.4%
				Seine				
Northern	1	60	12	−0.751**	−0.0859	5.06	3.17	−1.89
	3	72	11	−0.721*	−0.0877	4.80	2.88	−1.92
	4	85	10	−0.701*	−0.0636	4.37	2.97	−1.40
Hecate Strait	2E	47	12	−0.652*	−0.0639	4.62	3.28	−1.34
	5	150	12	−0.701*	−0.0665	4.60	3.13	−1.47
	6	274	12	−0.751**	−0.0807	4.83	3.05	−1.78
Central	7	90	12	−0.787**	−0.0683	4.37	2.87	−1.50
	8	311	12	−0.759**	−0.0607	4.29	2.95	−1.34
	9	43	9	−0.820**	−0.0820	4.61	2.80	−1.81
	10	7	5	−0.918*	−0.0824	4.61	2.79	−1.82
District 2 means					−0.0712	4.57	3.01	−1.57
Johnstone Strait, etc.	12	189	12	−0.839**	−0.0728	4.54	2.94	−1.60
	13	18	12	−0.792**	−0.0656	4.69	3.25	−1.44
West coast of Vancouver I.	25	2	5	−0.338	−0.0355	4.20	3.42	−0.78
	26	2	4	−0.609	−0.0839	4.23	2.39	−1.84
District 3 means					−0.0719	4.55	2.97	−1.58
Overall means					−0.0713	4.57	3.00	−1.57
Percentage change								−34.4%
				Troll				
Northern	1	60	12	−0.688*	−0.0791	5.26	3.52	−1.74
	3	72	12	−0.716**	−0.0871	5.47	3.55	−1.92
	4	85	11	−0.781**	−0.1060	5.75	3.42	−2.33
Hecate Strait	2E	47	10	−0.579	−0.0679	5.33	3.84	−1.49
	5	150	11	−0.876**	−0.1094	5.71	3.30	−2.41
	6	274	10	−0.875**	−0.1309	5.93	3.05	−2.88
Central	7	90	12	−0.878**	−0.0979	5.44	3.29	−2.15
	8	311	12	−0.878**	−0.1056	5.73	3.40	−2.33
	9	43	6	−0.652	−0.1329	5.93	3.01	−2.92
	10	7	7	−0.770*	−0.1306	5.86	2.99	−2.87
District 2 means					−0.1087	5.70	3.31	−2.39
Johnstone Strait, etc.	11	2	8	−0.912**	−0.1596	6.42	2.91	−3.51
	12	189	12	−0.923**	−0.1182	5.67	3.07	−2.60
	13	18	7	−0.860*	−0.1041	5.48	3.19	−2.29
West coast of Vancouver I.	23	1	7	−0.680	−0.0824	5.75	3.93	−1.82
	25	2	7	−0.543	−0.0834	5.47	3.64	−1.83
	26	2	8	−0.753*	−0.1204	6.24	3.59	−2.65
	27	10	11	−0.793**	−0.0895	5.49	3.52	−1.97
District 3 means					−0.1157	5.66	3.11	−2.55
Overall means					−0.1099	5.70	3.28	−2.42
Percentage change								−42.4%

catching power lies closer to the modal size of the odd-year fish than to that of the even-year fish. (2) The rate of decrease in size of pinks caught by gill net is significantly less than that of those caught by seine. This can be a result of the gill-netters failing to keep up to date with the decline in size by shifting to smaller mesh when fishing for pinks, while those caught in sockeye nets would increasingly tend to come from the upper part of the pinks' range. (3) Comparing different fishing areas, there is some tendency for the rate of decrease in size of pink salmon to be large in areas where the fraction of the total catch taken by gill net is large, particularly in odd years (Fig. 4).

ORIGIN OF THE DECLINE

There are a number of estimates of pink salmon sizes in

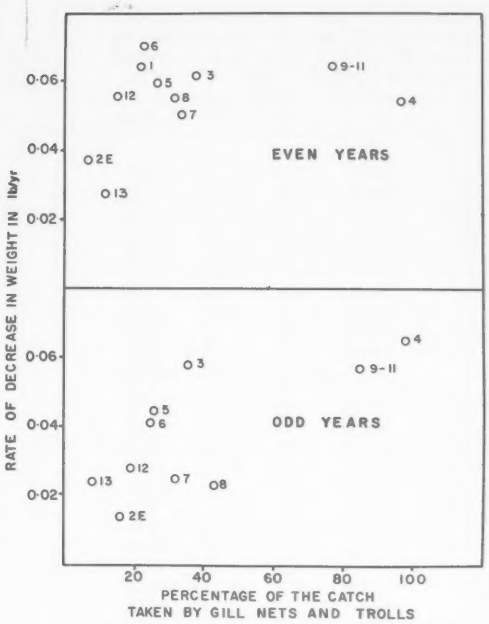

FIG. 4. Abscissa: percentage of the pink salmon catch in different statistical areas (indicated by numbers by the points) that is taken by selective fishing gears (gill nets and trolls). Ordinate: rate of decrease in weight of the fish in pounds per year.

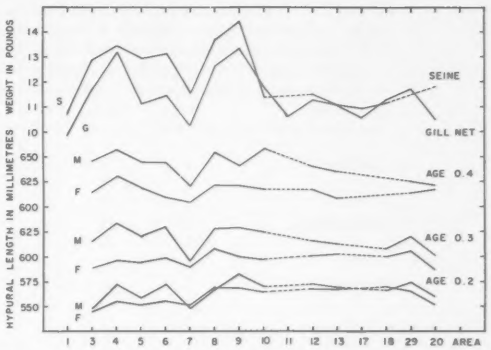

FIG. 5. Mean computed 1963 weights and lengths of chum salmon caught in British Columbia statistical areas, arranged from north to south.

catches made before 1951 which suggest that their sustained decline in size did not begin until about 1950–52. It would seem that the gill-netters gradually shifted to a somewhat larger mesh when renewing their nets after payment by weight, starting in 1945, made the larger fish more valuable. Thus larger pinks started to be more heavily harvested than smaller ones. Notice that the initial effect of this shift would be to make the size of gillnetted pinks larger, not smaller. Only after the genetic effect had been in operation for a few generations would the size of pinks caught by gill net start to decrease.

Troll fishermen also capture pinks of larger than average size, and this selection became increasingly important during the later 1960s and early 1970s.

Chum Salmon

AGE COMPOSITION AND GILL NET SELECTIVITY

Chum salmon appear in the British Columbia commercial fishery at three main ages: toward the end of their 3rd, 4th, and 5th yr of life, i.e. at ages 2, 3, and 4. Age 3 is everywhere commonest, age 2 next, and age 4 rather uncommon except in the north. Unlike pink salmon, chum samples show no

TABLE 4. Trends in mean age of chums with time during 1956–1972, in statistical areas arranged from north to south. N = number of years of observations; r = correlation; b = rate of increase in age (yr/yr); 1963 = computed mean age in 1963. Means are weighted as in Table 5 (*$P < 0.05$).

District	Area	Catch	N	r	b	1963
2	3	45	16	0.426	0.00929	2.994
	4	15	15	0.500	0.01045	2.969
	5	17	16	0.343	0.01712	2.863
	6	59	14	0.535*	0.02809	2.774
	7	90	14	0.255	0.01159	2.703
	8	73	15	0.318	0.01668	2.763
	9	11	12	0.345	0.02591	2.717
	10	6	12	0.536	0.03787	2.642
3	12	111	14	0.444	0.01796	2.727
	13	83	14	0.321	0.01561	2.683
	18	6	6	0.581	0.04046	2.536
	23	18	5	0.837	0.03141	2.606
	20	9	15	0.533*	0.02982	2.536
1	29	53	15	0.393	0.01908	2.714
Weighted means						
District 2	—	—	—	—	0.01676	2.792
District 3 + 1	—	—	—	—	0.01920	2.693

TABLE 5. Trends in mean weight in pounds of chum salmon caught by two gears. N = number of years' data used; r = linear correlation coefficient; b = regression coefficient (lb/yr); 1951 and 1975 = computed sizes (lb) in the years indicated; change = computed change in size between 1951 and 1976 (lb). All means are weighted as the total 1951–75 catch in each area, rounded to the nearest million pounds (*$P < 0.05$, **$P < 0.01$).

Region	Area	Catch	N	r	b	1951	1975	Change
				Gill net				
Northern	1	6	21	−0.102	−0.0155	10.10	9.73	−0.37
	3	45	25	−0.127	−0.0150	11.85	11.44	−0.41
	4	15	25	−0.593**	−0.1155	14.58	11.81	−2.77
Hecate Strait	2E	42	24	−0.269	−0.0272	9.80	9.15	−0.65
	5	17	25	−0.176	−0.0234	11.43	10.87	−0.56
	6	59	25	−0.216	−0.0317	11.83	11.07	−0.76
Central	7	40	25	−0.025	−0.0033	10.31	10.23	−0.08
	8	73	25	−0.295	−0.0450	13.17	12.09	−1.08
	9	11	25	−0.456*	−0.1034	14.63	12.15	−2.48
	10	6	25	−0.155	−0.0212	12.05	11.54	−0.51
District 2 means					−0.0296	11.65	10.93	−0.71
Johnstone Strait, etc.	11	2	25	−0.231	−0.0308	11.01	10.27	−0.74
	12	111	25	−0.321	−0.0283	11.68	11.00	−0.68
	13	83	25	−0.379	−0.0442	11.64	10.58	−1.06
Georgia Strait	17	10	19	−0.330	−0.0322	11.00	10.23	−0.77
	18	6	19	+0.003	+0.0006	11.25	11.26	+0.01
Fraser	29AB	53	25	−0.530**	−0.0635	12.54	11.02	−1.52
Juan de Fuca	20	9	24	−0.206	−0.0194	10.71	10.24	−0.47
West coast of	23	18	17	−0.218	−0.0158	10.43	10.05	−0.38
Vancouver I.	24	5	12	−0.359	−0.0715	10.45	8.73	−1.72
	25	18	19	−0.247	−0.0236	10.80	10.23	−0.57
	26	8	13	+0.082	+0.0066	10.17	10.33	+0.16
	27	5	19	+0.498*	+0.0730	9.86	11.61	+1.75
District 3 and 1 means					−0.0347	11.55	10.72	−0.83
Overall means					−0.0320	11.60	10.83	−0.77
Percentage change								−6.6%
				Seine				
Northern	1	6	22	−0.262	−0.0417	11.24	10.24	−1.00
	3	45	25	−0.693**	−0.1113	14.21	11.54	−2.67
	4	15	14	−0.565*	−0.1564	15.31	11.55	−3.76
Hecate Strait	2E	42	23	−0.137	−0.0193	9.93	9.47	−0.46
	5	17	25	−0.696**	−0.1746	15.33	11.14	−4.19
	6	59	25	−0.341	−0.0667	13.95	12.35	−1.60
Central	7	40	25	−0.255	−0.0489	12.13	10.96	−1.17
	8	73	25	−0.492*	−0.1244	15.19	12.20	−2.99
	9	11	20	−0.405	−0.1156	15.84	13.07	−2.77
	10	6	15	−0.636*	−0.0663	12.21	10.62	−1.59
District 2 means					−0.0837	13.42	11.41	−2.01
Johnstone Strait, etc.	11	2	6	+0.531	+0.0590	9.72	11.14	+1.42
	12	111	25	−0.383	−0.0430	12.04	11.01	−1.03
	13	83	25	−0.304	−0.0318	11.49	10.73	−0.76
Georgia Strait	17	10	14	−0.033	−0.0029	11.02	10.95	−0.07
	18	6	18	+0.007	+0.0006	11.20	11.21	+0.01
Juan de Fuca	20	9	25	−0.683**	−0.1757	13.96	9.74	−4.22
West coast of	23	18	17	−0.239	−0.0281	10.82	10.15	−0.67
Vancouver I.	24	5	15	−0.309	−0.0459	10.60	9.50	−1.10
	25	18	21	+0.054	+0.0064	10.50	10.65	+0.15
	26	8	17	+0.066	+0.0072	10.49	10.66	+0.17
	27	5	12	+0.345	+0.0452	9.98	11.06	+1.08
District 3 means					−0.0336	11.58	10.77	−0.81
Overall means					−0.0600	12.55	11.11	−1.44
Percentage change								−11.5%

significant latitudinal difference in size at a given age within British Columbia (Fig. 5), but overall mean size tends to be less in the south (Table 5) because of the younger age composition indicated by Table 4.

A difference between chums and the other species is that gill nets tend to capture *smaller* chums than seines (Table 5).

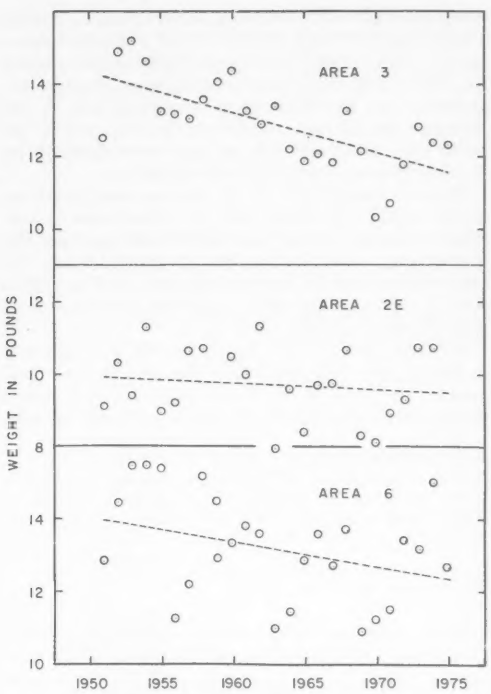

FIG. 6. Mean weights of chum salmon caught by seine in statistical areas 3, 2E, and 6.

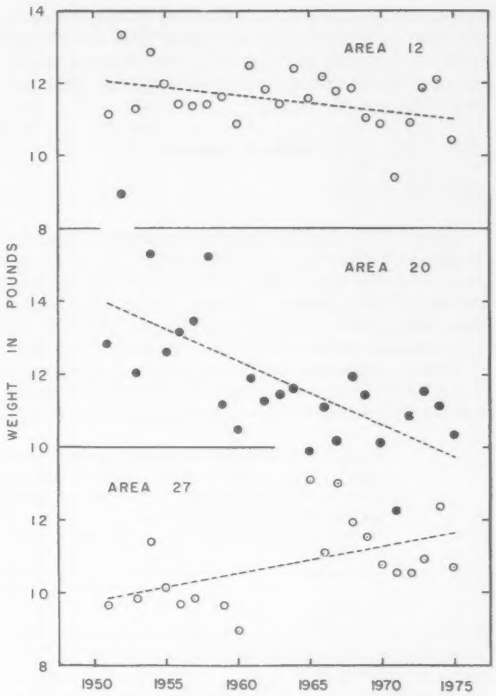

FIG. 7. Mean weights of chum salmon caught by seine in areas 12 and 20, and of those caught by gill net in area 27.

The reason is evidently that many chums are captured in nets for which the target species are sockeye or pink salmon, which average much smaller in size. Few chums are taken by trolling, so any troll selectivity is not a factor in determining changes in age or size. However, the gill net selectivity pattern suggests that mean age should have increased and, at least at first glance, that mean size also should have increased. The actual course of events has been somewhat different and it appears to have been quantitatively different in the two halves of the province.

CHANGES IN NORTHERN AREAS

In northern British Columbia (statistical district 2, including areas 3–10), the (weighted) average age in the catch increased by 0.38 yr from 1957 to 1972, because chums of age 2 became scarcer and age 4 became commoner (Table 4). The chums caught by gill nets averaged about 1.12 lb (0.51 kg) smaller than those caught by seines (Table 5), so presumably they harvested the younger fish more heavily, and this would make for an hereditary increase in mean age.

However, in spite of the increase in age, the *size* of chums seined in district 2 decreased by 2.0 lb (910 g) from 1951 to 1975, which is about 0.3 lb or 140 g per generation (Table 5, Fig. 6). This paradox can be related to the fact that, among chums and other salmon, age of maturity is negatively correlated with rate of growth. Thus in removing a higher proportion of the 3rd year chums, the gill nets were automatically removing the fastest-growing segment of the stock, so that genes for fast growth became scarcer in the population. On the other hand, selection *within* each age group, except possibly the youngest, would tend to increase the relative abundance of genes for faster growth. There is not enough information to construct a good quantitative model that includes all these processes, so a comprehensive explanation for the phenomenon of increasing age and decreasing size lies in the future. A contribution from environmental trends cannot be ruled out (Ricker 1980a, p. 20).

CHANGES IN SOUTHERN AREAS

In the southern part of the province (districts 1 and 3) the rate of increase in mean age of chum salmon has been similar to that in the north (0.37 yr in 24 yr). Because of a major slump in abundance during the 1960s, good data are available only for the Fraser and the migration-route areas 12, 13, and 20, and even there the catch decreased by about 90%. Figure 7 shows the trends in three areas. The 24-yr decrease was 1.0 lb (450 g) for chums seined or gillnetted in areas 12, 13, and 20, and 1.5 lb (680 g) for Fraser gillnetted chums (Table 5, Fig. 7). What few data there are suggest much less size difference between seined and gillnetted fish in the south than in the north; if this is reliable, it makes a selection explanation unlikely. What role, if any, the period of low

abundance may have played is unknown. A suggestion of an important effect of some sort may appear in the area 27 panel of Fig. 7: the chums that reappeared after the period of scarcity were much larger than those obtained up to 1960, contrary to the general trend.

Sockeye Salmon

Decrease in Size

Tables 6 and 7 show the changes in mean weight of sockeye caught in different areas since 1951. Only a few areas have even moderately large catches and the Fraser runs are much the largest in the province. Because of this variability, all mean values below are weighted by the total 1951–75 catch in the areas concerned, rounded to the nearest million pounds.

Table 8 summarizes the 24-yr changes in mean weight during 1951–75. It is a decrease of 0.46 lb (210 g) for seined fish and of 0.28 lb (130 g) for gillnetted fish. For both gears the decrease was larger in southern British Columbia (districts 1 and 3) than in the north (district 2). Line 3 of Table 8 shows the decreases in gill net sizes in areas which also have an entry for seines; it makes the contrast between the two gears greater. The reason for the difference is presumably that, as size decreased, the gill nets continued to catch fish of what had earlier been the optimum size, and there was considerable lag in adjusting mesh size to a decreasing optimum.

Figure 8 shows a series of size indexes based mainly on length samples. The index used is a combination of logarithms of mean length of each sex of each important life-history type, each sex and type being given equal weight. The longer period used for the regression lines in Fig. 8 gives some of the areas trends that are different from those of the sales-slip series (Fig. 9).

Notice the period of large size during 1950–54, especially in Fig. 8. This coincides with a time of low ocean temperature, as shown in the bottom panel, and it is mainly responsible for the negative relation between size and tem-

Table 6. Trends in mean weight in pounds of sockeye caught by gill net and seine. N = number of years' data used; r = linear correlation coefficient; b = regression coefficient (lb/yr); 1951 and 1975 = computed sizes (lb) in the years indicated; change = computed change in size between 1951 and 1975 (lb). Means are weighted by the total catch by all gears in each area, rounded to the nearest million pounds (*$P < 0.05$, **$P < 0.01$).

Region	Area	Catch	N	r	b	1951	1975	Change
				Gill net				
Northern	1	3	21	+0.546*	+0.0347	5.57	6.41	+0.84
	3	36	25	−0.042	−0.0021	6.26	6.21	−0.05
	4	97	25	−0.052	−0.0028	6.16	6.09	−0.07
Hecate Strait	5	11	25	−0.126	−0.0050	6.12	6.00	−0.12
	6	10	25	−0.353	−0.0280	6.82	6.15	−0.67
Central	7	4	25	+0.588**	+0.0472	4.82	5.95	+1.13
	8	17	25	+0.219	+0.0190	4.79	5.24	+0.45
	9	122	25	−0.150	−0.0164	6.09	5.70	−0.39
	10	38	25	−0.130	−0.0107	6.43	6.17	−0.26
	11	3	25	−0.292	−0.0242	6.53	5.95	−0.58
Johnstone Strait	12	67	25	+0.042	+0.0020	5.91	5.96	+0.05
	13	27	25	−0.014	−0.0008	6.12	6.10	−0.02
Georgia Strait	17	3	15	−0.123	−0.0090	6.40	6.18	−0.22
	18	9	20	−0.505*	−0.0328	6.62	5.83	−0.79
Fraser	29AB	134	25	−0.319	−0.0233	6.41	5.85	−0.56
Juan de Fuca	20	107	24	−0.344	−0.0227	6.49	5.94	−0.55
West Coast Vancouver I.	23	10	25	−0.409	−0.0153	5.13	4.77	−0.36
	24	9	12	+0.316	+0.0178	5.32	5.74	+0.42
Weighted means					−0.0117	6.19	5.91	−0.28
Percent change								−4.5%
				Seine				
Northern	1	3	18	+0.680**	+0.0438	4.84	5.90	+1.06
	3	36	25	−0.351	−0.0273	6.18	5.53	−0.65
Hecate Strait	5	11	25	−0.077	−0.0057	5.46	5.33	−0.13
	6	10	25	−0.182	−0.0191	5.65	5.19	−0.46
Central	7	4	25	+0.260	+0.0205	4.07	4.56	+0.49
	8	17	25	+0.171	+0.0175	4.21	4.63	+0.42
Johnstone Strait	12	67	25	−0.060	−0.0040	5.76	5.66	−0.10
	13	27	25	−0.209	−0.0172	6.10	5.69	−0.41
Georgia Strait	17	3	8	+0.239	+0.0184	5.79	6.23	+0.44
	18	9	15	−0.315	−0.0205	6.46	5.97	−0.49
Juan de Fuca	20	107	24	−0.326	−0.0383	6.58	5.66	−0.92
West Coast Vancouver I.	24	9	21	−0.248	−0.0129	5.62	5.31	−0.31
Weighted means					−0.0191	6.01	5.55	−0.46
Percentage change								−7.6%

TABLE 7. Trends in mean weight in pounds of sockeye caught by trolling. Symbols as in Table 6.

Region	Area	Catch	*N*	*r*	*b*	1951	1975	Change
Northern	1	3	19	+0.176	+0.0169	6.33	6.74	+0.41
Johnstone	12	67	22	−0.238	−0.0220	6.82	6.29	−0.53
Strait	13	27	8	−0.188	−0.0215	6.69	6.17	−0.52
West coast	23	10	22	−0.085	−0.0071	6.46	6.29	−0.17
Vancouver I.	24	9	23	−0.158	−0.0121	6.60	6.31	−0.29
	25	3	19	+0.025	+0.0028	6.45	6.52	+0.07
	27	5	21	−0.199	−0.0184	6.58	6.14	−0.44
Weighted means					−0.0187	6.88	6.42	−0.46
Percentage change								−6.7%

TABLE 8. Changes in weighted mean size of sockeye over the 24 yr 1951−75, and (in line 4) the mean size difference between seined and gillnetted fish. Data from Table 6.

	North (areas 1−11), lb	South (areas 12−29), lb	Total (areas 1−29), lb
1. Seined[a,b]	−0.21	−0.55	−0.46
2. Gillnetted[a]	−0.18	−0.38	−0.28
3. Gillnetted[b]	+0.06	−0.27	−0.18
4. Size difference[b]	0.59	0.15	0.27

[a]Includes all areas where data are available.
[b]Includes areas where there are data for both gill nets and seines.

perature described in the Effects of Changes in the Environment section. However, a period of even lower temperature in 1969−72 did not produce any comparable increase in sockeye size.

Effect of Age Composition on Rate of Decrease

If the decreases in size of sockeye shown in Table 8 are a result of fishery selection, we should, at first glance, expect the region of more rapid decrease (the south) to have the greater difference in size between seined and gillnetted fish. Line 4 of Table 8 shows that the reverse is true. This results from the difference in age composition in the two regions. In the north two ocean ages enter the catch in more or less equal numbers, the older and larger having a slower growth rate. Thus selection that favors more small fish in the spawning stock also favors faster growth, and the net change in mean size is unpredictable. Southern sockeye, on the other hand, are dominated by Fraser fish, where one ocean age far exceeds all others. Thus the contrast between ages plays no significant role in the south, and the Fraser fish have in fact decreased more in size, in spite of their smaller intensity of selection indicated by the smaller size difference between gillnetted and seined fish.

Compared with pink and coho salmon, the decrease in size of sockeye has not been very large in any region; in fact, when the years 1976−79 are added to the series (Fig. 9), none of the trends in mean weight are "significant." This can be ascribed partly to the two opposed effects of selection in the north where two major ocean age groups are present, and also to the low intensity of selection in the south. Another aspect of selection that opposes the decline in both regions is the fact that "jacks" (age-3 spawners) are only weakly harvested in comparison with the older fish. These are the faster-growing members (on the average) of the male sex, so their being favored for reproduction has helped to maintain growth rates in stocks where they occur in significant numbers. Their numbers are greatest and have increased importantly in the Birkenhead stock on the Fraser and some of the Babine stocks on the Skeena (Ricker 1976).

An event that tended to *increase* size and age on the Skeena was the major mortality at an obstruction in 1951 and 1952. This killed a greater percentage of the smaller and younger sockeye than of the larger and older ones (Godfrey et al. 1954).

Still another factor retarding decrease in size may be the temperature effect. For example, on the Fraser (area 29) the observed 24-yr decrease was 0.56 lb or 250 g (Table 6); but if temperature tended to *increase* size by 0.44 lb (200 g), as described in the Effects of Changes in the Environment section, the unopposed effect of selection would have been a decrease of $0.56 \pm 0.44 = 1.00$ lb (450 g).

Changes in Relative Size of Different Ages

Foskett (1958) compared the size distribution in the gill net catch with that in the escapement at Owikeno and found that fish near the median size were much more heavily exploited. The spawning stock thus contained an excess of the larger of the fish of ocean age 4 and of the smaller of the fish of ocean age 3, as compared with the unfished stock. Todd and Larkin (1971) found a similar situation on the Skeena. Given some, even quite incomplete, segregation of the two ages in time or place of spawning, this results in a gradual increase in the size of the sockeye of ocean age 4 and a gradual decrease in the size of those of ocean age 3. Godfrey (1958) showed that this

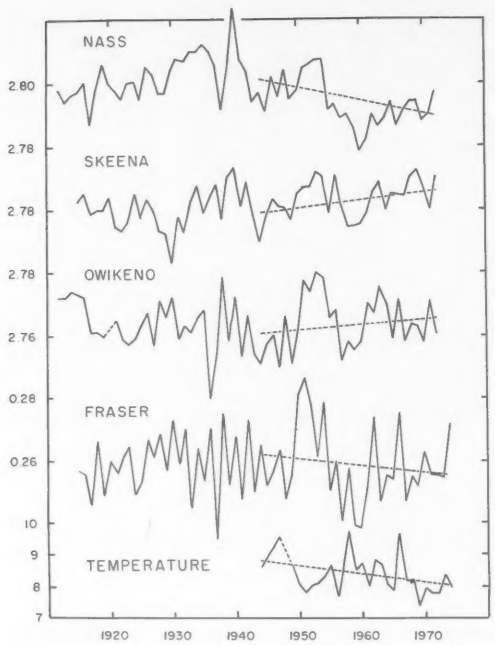

FIG. 8. Trends in size of sockeye runs in four areas, and the August-through-July mean ocean surface temperature at station P (50°N, 145°W). Regression lines are fitted to the period from 1944 onward. Ordinate units are as follows: for Nass, Skeena, and Owikeno: base-10 logarithms of fork length in millimetres; for Fraser: one-third of the base-10 logarithm of weight in pounds; for temperature, degrees Celsius.

change did occur gradually over the years from 1910 to 1949 at Skeena and Owikeno. Ricker (1981) brought the length series up to 1972, and included the Nass (area 3). The amount of change in the *difference* in weight between fish of ocean age 3 and ocean age 4, over 39 yr, can be estimated from Godfrey's graphs as follows:

	Males, g	Females, g
Skeena	540	320
Owikeno	730	500

Coho Salmon

In one respect coho salmon present a simpler situation than chums or sockeye in that most of them mature after 2 yr of ocean growth. An appreciable number of males mature as "jacks" after only one season in the ocean, but these are not large enough to appear in the commercial fishery and are not important even in the sport fishery. However, cohos differ from pinks, chums, and sockeye in that they are harvested throughout the time they are making rapid growth during their last year of life. Hence the time at which fishing operations occur must be considered in comparing mean annual sizes of

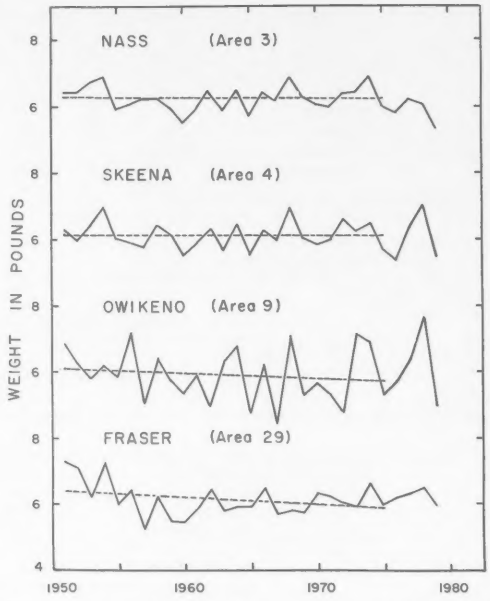

FIG. 9. Mean weight in pounds of sockeye caught by gill net in four areas. Regression lines are fitted to the years 1951–75 only.

cohos caught by different gears or in different years.

AREAS OUTSIDE OF THE SOUTHERN STRAITS

Table 9 shows the mean size and rate of decrease in size of cohos caught by three gears during 1951–75; Fig. 10 illustrates some of the trends. Gillnetted fish are larger than seined fish and troll-caught fish are sometimes larger, sometimes smaller (Fig. 11). However, the commercial trolls start making important landings 4 or 5 wk earlier than the nets. If catches made in any given month are compared, the trolls usually take the largest fish (Table 10; see also Table 6 of Ricker and Wickett (1981)). In terms of potential weight at maturity, troll-caught cohos averaged 1.1 lb (500 g) larger than seined cohos, and gillnetted cohos were 0.75 lb (340 g) larger than those taken by seine.

The decrease in mean seasonal size was about 25% or 2.23 lb (1010 g) between 1951 and 1975, and this represents about 2.7 lb (1220 g) when converted to size at maturity. From 1975 to 1979 there has been an additional decrease of about 0.3 lb, for a total of 3.0 lb (1360 g). Catches of all three fishing gears have exhibited about the same amount of decrease (Table 9), indicating that the fish available have become smaller.

Selection of the larger fish by trolls and gill nets can produce a change in the genetic composition of coho stocks by leaving smaller-than-average individuals for reproduction. From this point of view, the 2.7-lb (1220-g) decrease in size of cohos outside the Straits, corresponding to 0.37 lb (168 g) per generation, represents the response to selection (R). The mean size difference between cohos caught by selective gears (trolls and gill nets) and those caught by seines is estimated to

TABLE 9. Trends in mean weight in pounds of cohos caught by three gears. N = number of years' data used; r = linear correlation coefficient; b = regression coefficient (lb/yr); 1951 and 1975 = computed sizes (lb) in the years indicated; change = computed changes in size between 1951 and 1975 (lb) (*$P < 0.05$, **$P < 0.01$).

Region	Area	N	r	b	1951	1975	Change
			Gill net				
Northern	3	25	−0.611**	−0.0669	9.57	7.97	−1.60
	4	25	−0.720**	−0.0791	9.31	7.41	−1.90
Hecate Str. W.	2E	21	−0.485*	−0.0736	10.45	8.68	−1.77
Hecate Str. E	5	25	−0.717**	−0.0780	9.39	7.52	−1.87
	6	25	−0.726**	−0.1055	10.09	7.56	−2.53
Central mainland	7	25	−0.698**	−0.0639	9.79	8.25	−1.54
coast	8	25	−0.432**	−0.0445	10.30	9.23	−1.07
	9	25	−0.702**	−0.0860	9.68	7.63	−2.06
	10	25	−0.636**	−0.0663	8.47	6.88	−1.59
Johnstone Strait,	11	25	−0.498**	−0.0857	9.18	7.13	−2.05
etc.	12	25	−0.815**	−0.1178	10.32	7.49	−2.83
	13	25	−0.707**	−0.1114	9.99	7.32	−2.67
Strait of	17	20	−0.412	−0.0842	9.46	7.44	−2.02
Georgia	18	22	−0.373	−0.0755	9.85	8.04	−1.81
Fraser River	29	25	−0.137	−0.0152	7.63	7.27	−0.36
Outer Coast NW	1	22	−0.617**	−0.1148	9.56	6.80	−2.76
West coast	27	21	−0.852**	−0.2036	10.01	5.12	−4.89
Vancouver I.	25	15	−0.496	−0.0647	11.33	9.77	−1.56
	23	18	−0.721**	−0.1355	10.98	7.73	−3.25
Juan de Fuca	20	24	−0.283	−0.0416	8.79	7.79	−1.00
Mean				−0.0857	9.70	7.65	−2.05
Percentage change							−21.1%
			Seine				
Northern	3	25	−0.387*	−0.0394	7.31	6.36	−0.94
Hecate Str. W	2E	24	−0.203	−0.0417	9.05	8.05	−1.00
Hecate Str. E	5	25	−0.617**	−0.0733	8.73	6.97	−1.76
	6	25	−0.693**	−0.0897	8.30	6.65	−2.15
Central mainland	7	25	−0.718**	−0.0857	8.54	6.49	−2.05
coast	8	25	−0.177	−0.0191	7.62	7.16	−0.46
	9	21	−0.647**	−0.1867	8.39	3.91	−4.48
Johnstone Strait,	12	25	−0.762**	−0.1056	9.81	7.28	−2.53
etc.	13	25	−0.626**	−0.0865	9.40	7.33	−2.07
Strait of Georgia	17	7	−0.514	−0.1214	9.24	6.32	−2.92
	18	10	−0.016	−0.0037	7.69	7.60	−0.09
Outer Coast NW	1	23	−0.758**	−0.1720	10.83	6.70	−4.13
West coast	27	11	−0.770*	−0.1339	9.74	6.52	−3.22
Vancouver I.	26	17	−0.676**	−0.1120	11.20	8.51	−2.69
	25	20	−0.585**	−0.0964	11.11	8.80	−2.31
	24	16	−0.664**	−0.1443	10.42	6.95	−3.47
	23	10	−0.597	−0.1210	11.34	8.44	−2.90
Juan de Fuca	20	24	+0.015	+0.0027	7.42	7.49	+0.07
Mean				−0.0905	9.26	7.08	−2.17
Percentage change							−23.5%
			Troll				
Northern	3	25	−0.334	−0.0553	9.72	8.40	−1.32
	4	25	−0.579**	−0.0732	8.65	6.89	−1.76
Hecate Str. W	2E	25	−0.087	−0.0153	7.98	7.62	−0.36
Hecate Str. E	5	25	−0.692**	−0.0841	8.64	6.62	−2.02
	6	25	−0.897**	−0.1925	10.25	5.63	−4.62
Central	7	25	−0.578**	−0.0865	8.84	6.77	−2.07
mainland coast	8	25	−0.800**	−0.1727	10.59	6.44	−4.15
	9	25	−0.726**	−0.1286	9.58	6.50	−3.08
	10	23	−0.815**	−0.2346	10.91	5.28	−5.63
Johnstone Strait,	11	25	−0.740**	−0.1292	8.60	5.49	−3.11
etc.	12	25	−0.682**	−0.0892	7.86	5.72	−2.14
	13	25	+0.105	+0.0079	5.10	5.29	+0.19

Table 9. (*Concluded*)

Region	Area	*N*	*r*	*b*	1951	1975	Change
Strait of Georgia	17	25	+0.426*	+0.0287	3.87	4.56	+0.69
	18	13	+0.114	+0.0146	5.61	5.97	+0.36
Outer Coast NW	1	25	−0.517**	−0.0680	8.89	7.25	−1.64
West coast	27	25	−0.727**	−0.1122	8.83	6.13	−2.70
Vancouver I.	26	25	−0.710**	−0.1153	8.67	5.91	−2.76
	25	25	−0.711**	−0.1302	9.19	6.07	−3.12
	24	25	−0.605**	−0.0960	8.58	6.28	−2.30
	23	25	−0.581**	−0.0838	8.16	6.15	−2.01
	21	25	−0.565**	−0.0944	8.62	6.35	−2.27
Juan de Fuca	20	24	−0.507*	−0.0851	8.70	6.66	−2.04
Mean				−0.0907	8.44	6.27	−2.17
Percentage change							−25.7%

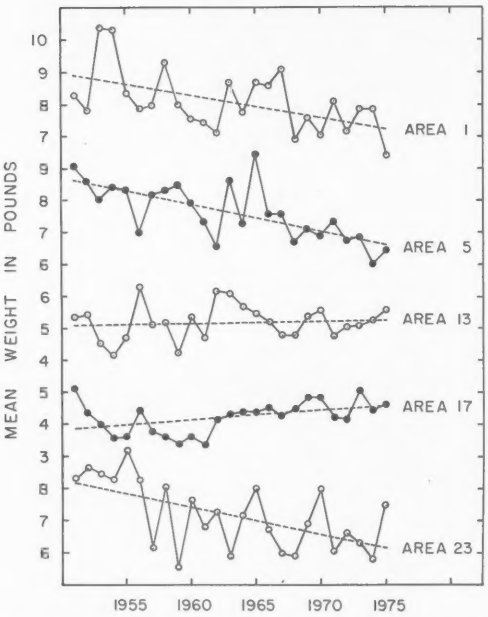

FIG. 10. Mean weight of cohos caught by troll in five statistical areas, with linear trend lines.

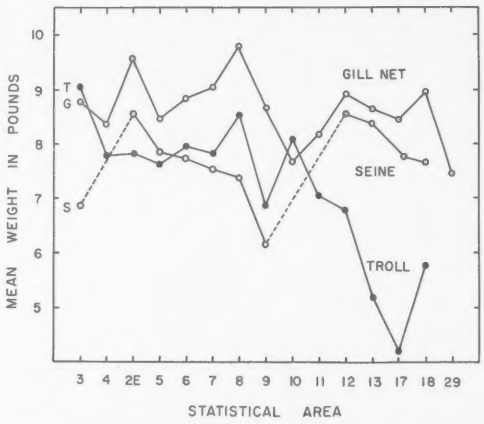

FIG. 11. Computed mean weight in 1963 of cohos caught by three different gears in statistical areas of the British Columbia mainland coast and adjacent Straits, arranged from north to south.

be about 1.0 lb (450 g). Given that the rate of mortality from fishing (including shaker loss) is 75−85%, age-3 spawners are estimated to be 1.1−1.6 lb (500−730 g) smaller than in a stock that is not fished, which is the selection differential (*S*). This means that the heritability of adult size, the ratio *R*/*S*, lies between 0.23 and 0.35, which is a reasonable range of values. Hence it is quantitatively possible that "outside" cohos decreased in size because of selection by the fishery.

LOWER JOHNSTONE STRAIT AND THE STRAIT OF GEORGIA (AREAS 13−18)

These Straits contain both a population of "native" cohos and fish that migrate into them from outside to ascend tributary streams. The local cohos grow more slowly than the outside ones. Apparently the locals are more vulnerable to trolling gear, for in these Straits the average size of troll-caught cohos is less than that of the seined or gillnetted fish (Fig. 11). The latter are taken mainly in August and September, and are presumably mostly from outside (Table 10). Another difference is that the troll catch in the Strait of Georgia and Lower Johnstone Strait did not exhibit any sustained trend in size from 1951 to 1975 whereas the seined and gillnetted cohos decreased similarly to non-Strait areas (Tables 9, 10). From 1975 to 1979, however, the Straits' troll-caught cohos did become somewhat smaller, perhaps only a temporary fluctuation.

There are several possible reasons why cohos resident in Lower Johnstone and Georgia Straits did not decrease in size up to 1975, in spite of selection by the commercial troll fishery. One possibility is that the noncommercial troll fishery, which now captures many more cohos in these Straits than commercial trollers (Argue et al. 1977), may have selection characteristics different from the commercial fishery

TABLE 10. Sizes of cohos caught in individual months by gill nets (GN), seines (S), and trolls (T), between 1951 and 1975. Symbols as in Table 9 (*$P < 0.05$, **$P < 0.01$).

Region	Area	Month	Gear	N	r	b	1951	1963	1975	Change
Outer coast, NW	1	9	GN	17	−0.157	−0.0240	9.89	9.60	9.31	−0.58
			S	11	−0.510	−0.1191	11.03	9.60	8.17	−2.86
			T	25	−0.573**	−0.0703	11.57	10.73	9.88	−1.69
Outer coast V. I.	23	9	GN	11	−0.781**	−0.0911	10.83	9.74	8.64	−2.19
			T	25	−0.443*	−0.0711	9.87	9.02	8.16	−1.71
Central mainland	8	8	GN	24	−0.367	−0.0376	9.38	8.93	8.48	−0.90
			S	23	−0.466*	−0.0570	8.32	7.64	6.95	−1.37
			T	24	−0.821**	−0.1502	10.96	9.16	7.36	−3.60
Johnstone Str.	12	9	GN	25	−0.707**	−0.0819	11.31	10.32	9.34	−1.97
			S	25	−0.701**	−0.1018	11.26	10.04	8.81	−2.45
			T	25	−0.742**	−0.1268	11.35	9.83	8.31	−3.04
Str. of Georgia	16	7	T	24	−0.093	−0.0060	4.50	4.43	4.36	−0.14
Str. of Georgia	17	9	GN	9	−0.818**	−0.1936	8.71	6.39	4.06	−4.65
			T	22	+0.076	+0.0080	4.83	4.93	5.02	+0.19

TABLE 11. Trends in mean whole weight in pounds of chinook salmon caught by trolling. N = number of years' data used; r = linear correlation coefficient; b = regression coefficient (lb/yr); 1951 and 1975 = computed sizes (lb) in the years indicated; decrease = computed decrease in size between 1951 and 1975 (*$P < 0.05$, **$P < 0.01$).

Region	Area	N	r	b	1951	1975	Decrease
Mainland coast and straits							
Northern	3	25	−0.817**	−0.3501	20.87	12.47	8.40
	4	25	−0.926**	−0.4378	19.08	8.57	10.51
Hecate Strait	2E	25	−0.769**	−0.2388	18.71	12.98	5.73
	5	25	−0.893**	−0.3320	17.91	9.94	7.97
	6	25	−0.728**	−0.2265	16.25	10.81	5.44
Central	7	25	−0.507**	−0.1059	20.08	17.54	2.54
	8	25	−0.477**	−0.1795	18.57	14.26	4.31
	9	21	−0.905**	−0.4853	20.30	8.65	11.65
	10	21	−0.521*	−0.2174	16.02	10.80	5.22
	11	20	−0.259	−0.0920	15.22	13.01	2.21
Johnstone Strait	12	25	−0.717**	−0.2046	15.65	10.74	4.91
	13	25	−0.868**	−0.1655	12.03	8.06	3.97
S. Georgia and	17	25	−0.769**	−0.2078	10.23	5.24	4.99
Juan de Fuca	18	25	−0.863**	−0.3559	13.83	5.29	8.54
Straits	20	20	−0.671**	−0.2291	14.61	9.11	5.50
Fraser	29A+B	18	−0.517*	−0.1480	9.19	5.62	3.57
Outer coasts of the big islands							
Queen Charlotte Is.	1	25	−0.875**	−0.3315	22.13	14.17	7.96
	2W	25	−0.687**	−0.2451	22.30	16.42	5.88
Vancouver Island	27	25	−0.805**	−0.2132	19.94	14.82	5.12
	26	25	−0.645**	−0.1378	18.95	15.65	3.30
	25	25	−0.804**	−0.2078	18.60	13.62	4.98
	24	25	−0.666**	−0.1382	16.33	13.01	3.32
	23	25	−0.643**	−0.0861	13.29	11.23	2.06
	21	25	−0.783**	−0.1813	14.07	9.72	4.35
Means				−0.2299	16.84	11.32	5.52
Percentage decrease							32.8%

because it tends to use lighter gear and to operate closer to shore. Another possibility is that cohos of hatchery origin may be somewhat larger than "wild" cohos, and in the Straits, hatchery fish have increased in numbers over the past 2 or 3 decades.

STRAIT OF JUAN DE FUCA (AREA 20)

The cohos caught in area 20 resemble "outside" cohos in size but they have decreased in size much less rapidly than most outside cohos; in fact, there has been little size trend since 1957 in the catch of any of the three commercial gears (Table 9). Many of the area 20 fish are probably of Puget Sound origin and have received an increasing contingent from the numerous hatcheries in that region during the past 2 or 3 decades. Hence for them too the large size of the increasing numbers of hatchery-reared cohos may have opposed the selection characteristics of the commercial troll fishery.

Chinook Salmon

Decrease in Age and Size

Decrease in age and size of chinook salmon has occurred from California to Alaska. It began at least as early as the 1920s, probably earlier. The British Columbia trends in size from 1951 to 1975 are shown in Table 11. The overall mean decrease in 24 yr is about 5.5 lb (2.5 kg). However, size decreased more rapidly in the northern district 2 (where the fish were larger to start with) than in the south (Fig. 12). In the Strait of Georgia (areas 17 and 18) the downward trend in size ceased about 1961 (Fig. 12), at a mean weight about 6 lb (2.7 kg); in the Strait of Juan de Fuca (area 20) it stabilized about the same time (Table 11), but at the larger size of 10.5 lb (4.8 kg).

Causes of the Decrease

There are at least eight possible causes of the decrease in size and/or age of chinook salmon. The *first* is simply the fact that for some or all stocks troll fishing has increased in waters where the fish are feeding and growing. As more trolling is done, more chinooks of any given age are caught earlier in the season and fewer are left for later on. The result is a decrease in the average size of chinooks caught during the season as a whole.

A *second* cause of reduced size is the well-known "fishing-up effect," first described by Baranov (1916). The troll fishery for chinooks in some areas takes both maturing fish and those that will not mature in the current year. The fish that mature at greater ages are exposed to capture for 2, 3, or 4 yr whereas the youngest group (age 1 or "jacks") are exposed during only 1 yr, apart from occasional age-0 individuals taken incidentally to other fisheries. Hence as fishing effort increases, relatively more fish are caught at younger ages and fewer survive to be caught at older ages.

A *third* cause of decreasing size might be the reduction in relative abundance of stocks that were of a large average size or large average age under natural conditions, either because they were more heavily fished or because they were more vulnerable to environmental deterioration, particularly dams.

The *fourth* possible reason is that there may have been a change in the ocean environment that has reduced either the growth rate or the age of maturity of chinook stocks, or both.

The *fifth* possible reason for a decrease in mean size is a slow change in the genetic makeup of a stock because of the tendency to take more of the older fish in the catch. This is mainly for the reason indicated under cause 2 above, but perhaps also because the larger (hence older) fish may be taken in greater numbers even by fisheries that attack only maturing specimens. The result is that there is increased representation of younger fish among breeding individuals, and continued over many years this can cause a gradual decline in the average age of the stock as a whole, both catch and spawners.

The *sixth* cause of a change in mean size is also genetic, due to probable selection of larger fish *of any given age* by the fishery. This tends to decrease the stock of genes that favor fast growth; but at present this effect is opposed by the fact

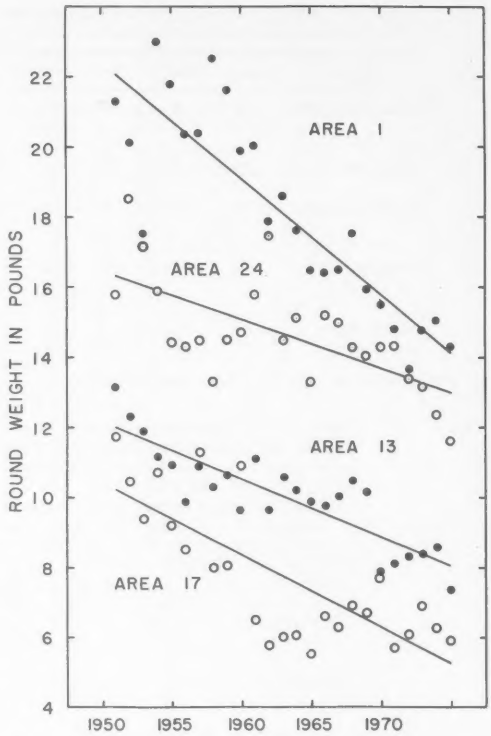

Fig. 12. Mean weights of troll-caught chinook salmon in four statistical areas, with linear trend lines.

that early maturing chinooks, which are favored by cause 5, grow faster than those that mature at an older age.

A *seventh* cause of change in size of chinook salmon is change in the kinds of fishing carried on and the regulations governing them. This includes such legal changes as the abolition of trap fishing, restrictions on places and times of commercial fishing, and size limits. It also includes the increase in troll gear at the expense of other types and, in the southern Straits, the increase in sport fishing in relation to commercial fishing.

An *eighth* possible cause of change might be some aspect of artificial propagation. For example, there could be faster (or slower) marine growth as a result of early life in the hatchery or there may have been conscious or inadvertent selection of hatchery spawners for either large or small size.

The first two causes of decrease in size of chinooks are self-evident. They are undoubtedly responsible for a major part of the decrease that has been observed. Cause 2 is very important in places, like area 23 or the Strait of Georgia, where large numbers of nonmaturing chinooks are caught. In areas such as 1, 2W, and 27, the early tagging experiments showed that the fish being caught were nearly all in their final year of life, although this may have changed now that the

average size is much smaller. In any event, if there are stocks living in places where they are not exposed to capture until they undertake their homeward migration, they are of course not affected by cause 2.

Cause 3, the selective reduction of runs containing fish larger or older than average, has probably occurred in the Columbia River, whose chinooks are captured off Canada as well as in United States waters. The summer chinooks of the Columbia are and were the largest in individual size. Originally they were also the most abundant group, but by the 1920s they had become much less numerous than either the spring or the fall chinook run, and the greater part of this remnant was finally exterminated by the Grand Coulee Dam. Kane (1968, p. 218) reported that in 1847 at Kettle Falls near Fort Colville the summer fish averaged 30 lb (14 kg) each, and that the previous autumn their spent carcasses along the upper Columbia occurred "in such vast numbers as literally to poison the atmosphere."

As regards cause 4, the large effects produced by the other causes, particularly Nos. 2 and 5, make it difficult to detect the much smaller changes that might reasonably result from ocean conditions. That the major trend toward smaller size of chinooks has nothing to do with a trend in ocean temperature is indicated by the fact that it started during a regime of ocean warming, up to 1940, and has continued during the cooling phase that has existed since that time.

Change in the Genetic Basis of Age of Maturity

Experiments in the State of Washington have demonstrated clearly that age of maturity is partly heritable; the data were summarized by Ricker (1972, Tables 11 and 12). It is even possible to make an estimate of this heritability from those of Lauren Donaldson's experiments in which the male and female parents were of the same age. Mean ages of the progeny were as follows:

Year-class	Parental age (both sexes)	Mean progeny age		
		Male	Female	Mean
1955	3	2.63	3.59	3.11
1963	3	2.83	3.63	3.23
1964	4	3.05	3.82	3.44

Progeny ages are of the individuals that returned to their home at the University of Washington. If the catch could be included, with each fish projected to its natural age of maturity, the mean progeny ages would be greater because a larger percentage of the later-maturing individuals had been harvested. This might increase the mean progeny ages by up to 0.2−0.3 yr, and it would affect later-maturing individuals somewhat more than earlier-maturing ones because they are vulnerable for a longer time. In any event, the mean progeny age is less for males than for females, as expected; and also as expected, the mean age of the two sexes (with or without the adjustment above) in each case "regresses" toward a population average that was intermediate between age 3 and age 4. In these experiments we can consider the selection differential (S) to be the 1-yr difference between the parental ages while the response (R) is the mean difference between the ages of their progeny.

Ideally the comparison should be between the progeny of fish of different ages spawned *in the same year*, so that the progeny would be exposed to the same environmental conditions. We do not have this situation but can average two comparisons from different years. Comparing the 1955 and 1964 year-classes in the schedule above, $R/S = 0.42$ for males and 0.23 for females; comparing 1963 and 1964, $R/S = 0.22$ for males and 0.19 for females. The geometric mean is 0.25. This must have a small negative bias from cause 2, as explained in the previous paragraph. A heritability of 0.25−0.3 is sufficient to make a substantial contribution to the decrease in mean age of maturity among chinook salmon, which is of the order of 1.5 yr since the 1920s.

Change in the Genetic Basis of Rate of Growth

It is scarcely necessary to demonstrate that growth rate in chinook salmon is partly heritable, although this has in fact been done by Donaldson (1970). Unfortunately we do not know whether the genetic makeup of today's chinook stocks favors a growth rate different from the primitive one. Fraser (1921), Parker and Larkin (1959, Fig. 14), and others have shown that in chinook salmon, as in other *Oncorhynchus*, later-maturing individuals grow more slowly than the early-maturing ones. Thus the strong selection by the fishery (especially by cause 2 above) that favors early maturity tends to *increase* the relative abundance of genes favoring more rapid growth. This would be opposed by a direct effect of selection against rapid growth by trolls and gill nets *if* they take more of the large fish of any given age. The net result may be a standoff, or the genes for more rapid growth may be on the increase. This latter would mean that chinooks *of any given age* are tending to become larger than formerly, even while the average size of the fish in both catch and escapement continues to decrease because older fish are becoming scarcer. But in the future, when average age has been reduced about as far as it can be, the direct effect of selection by size will come to the fore and growth rate will either start to decrease or the then prevailing rate of decrease will be accelerated.

All genetically based changes in chinooks have of course tended to become more rapid with the decrease in mean generation time.

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The Stock Concept and its Application to British Columbia Salmon Fisheries[1]

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The application of the stock concept to the management of British Columbia salmon fisheries is examined in an historical context. Early recognition of the distinctiveness of runs proceeding to different rivers led to the management principle that stocks should be harvested at a rate commensurate with their abundance level and their particular reproduction rate. Past and current work has been directed largely to applying this principle and included stock identification and estimates of abundance (catch and escapement) and of age composition. However, the application of the stock concept to management has been fraught with difficulties mainly because of the large number of stocks involved, the increasing catching power of the fishing fleet, and its displacement into fishing areas where stocks are mixed extensively. Some options for future management strategies are considered, but prospects for the maintenance of all but the most productive stocks seem dim.

Key words: Pacific salmon, stock concept, management, fisheries, stock–recruitment relationship

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Nous examinons dans un contexte historique l'application du concept de stocks à la gestion de la pêche des saumons de la Colombie-Britannique. Le fait qu'on ait tôt reconnu que les remontées dans les différentes rivières étaient distinctes a conduit à l'adoption du principe de gestion selon lequel les stocks devraient être récoltés à un taux correspondant à leur niveau respectif d'abondance et à leur taux de reproduction particulier. Les recherches passées et en cours sont en grande partie orientées vers l'application de ce principe et incluent l'identification des stocks, ainsi que des estimations d'abondance (prises et échappement), et composition par âge. Cependant, l'application à la gestion du concept de stocks a rencontré beaucoup de difficultés, surtout à cause du grand nombre de stocks impliqués, de la puissance de capture accrue de la flottille de pêche et des mouvements de cette dernière vers des lieux de pêche où il y a mélange intensif des stocks. Nous examinons certaines options de stratégies de gestion pour l'avenir, mais les perspectives de maintenir tous les stocks, sauf les plus productifs, sont peu encourageantes.

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SALMON fishing on a commercial scale began in British Columbia in the 1830s to meet local needs and a small export market for salted fish. With the development of the canned product, a large export market was created and the salmon fishery expanded rapidly. In 1866, the first cannery was operated on the Fraser River. By the turn of the century there were 65 canneries along the British Columbia coast.

Since these early days, the demand for salmon has remained strong and has resulted in continuing intense competition between processors and between fishermen for a larger catch and larger share of these fish.

The current salmon fishery is the most dynamic and valuable one on Canada's west coast. Each year, incoming salmon are met by a fleet of over 5000 mobile and efficient fishing vessels. The resulting catch is close to 23 million annually, worth approximately $150 million to the fishermen. There is also a vigorous sport fishery, with catches in recent years probably lying between 1 and 1.5 million annually.

Early Application of the Stock Concept

From the outset of commercial salmon fishing in British Columbia there was some appreciation of the stock concept. Immigrants from Europe who became involved as fishermen, processors, or government officials brought with them the then current knowledge and management philosophy developed for Atlantic salmon (*Salmo salar*). In general, the present day concept was already formed at that time. Species were considered separately, as were runs within species to the

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different rivers. Differences in abundance and migration times were recognized.

The first reference to the stock concept as a basis for management of the British Columbia salmon fishery that I have uncovered is contained in 1880 and 1881 reports by A. C. Anderson, Inspector of Fisheries for British Columbia (Anderson 1880, 1881). In these reports, Anderson clearly reveals the concept that salmon stocks to major B.C. rivers are discrete, that the supply of salmon available varies from river to river, and he notes the relationship between the number of parent spawners and the resulting return to the fishery. When discussing Fraser River sockeye (*Oncorhynchus nerka*) Anderson wrote as follows: "The number of young fish descending to the sea in each succeeding summer to reascend after attaining maturity would necessarily depend greatly on the number of fish which reached the spawning beds during the preceding autumn." Somewhat later Fisheries Commissioner John Peace Babcock (Babcock 1902) advanced the concept of a stock–recruitment relationship and an optimum number of spawners to provide a maximum sustained yield when recommending regulation of the Fraser River sockeye fishery. He wrote, "The placing of restrictions on salmon fishing is justified only upon the ground that they are necessary in order to allow enough fish each year to reach the spawning grounds to ensure perpetuation. To be effective in this regard, regulations governing fishing on a river should be framed so as to conform to the conditions which exist upon that particular stream."

Anderson and his successor Babcock firmly established the stock concept as a basis for managing British Columbia's salmon fishery. They recognized that stocks to the different rivers of B.C. were discrete and varied in abundance and migration time, that there was a relationship between spawners and recruits, and that rivers differed in the numbers of salmon they could produce and that the catch must be regulated accordingly. The regulatory action they recommended reflected their views, and included limiting fishing effort, restricting seasonal and weekly fishing periods, and restricting fishing gear.

Data for Management

In the years following the reports of Anderson and Babcock and through to the present, the main energies of salmon workers in B.C. have been directed to provide the basic biological information needed to apply the stock concept to fisheries management. They have focused on the identification of stocks, their migration routes and times, their abundance (catch and escapement), and age at return (to relate return to brood years).

Stock Identification

Various methods have been used to distinguish stocks, including scale characters, meristics and morphometrics, parasites, and tagging. The one used most extensively and successfully has been the tagging and marking of adults or juveniles, with subsequent recovery in the catch or on the spawning grounds. Adult taggings in 1918 (O'Malley and Rich 1920) and in 1925 (Williamson 1927) provided information on the migratory route of sockeye bound for the Fraser River. Another 1925 tagging (Williamson 1927) provided similar information for Nass and Skeena river sockeye. Tagging of chinook (*O. tshawytscha*) and coho (*O. kisutch*) began in 1925 (Milne 1957), and that of pink (*O. gorbuscha*) and chum (*O. keta*) in 1928 (Pritchard 1930, 1932).

Since these early programs, there have been scores of taggings on adults carried out along migration routes, in fishing areas, and in rivers and streams. A compilation of marine tag recovery programs carried out between 1925 and 1977 (Anon. 1978) lists 31 taggings of pinks, 17 of coho, 16 of chinook, and 28 each of chum and sockeye. A summary of adult taggings in freshwater has not been made, but the number is probably close to that for marine taggings.

The tagging or marking of juvenile Pacific salmon from known spawning or nursery areas with subsequent recovery at later life history stages has been practiced since about the turn of the century. In 1896, 5000 juvenile chinook were marked and released from the Clackamas (Oregon) hatchery (Gilbert 1913). Chamberlain (1907) reported the release in 1903 of marked sockeye fry into the Noka River in Alaska. Juvenile marking programs did not begin in British Columbia until the 1930s, when Pritchard (1938, 1939) marked and released pink fry to assess a transplant experiment and to measure the degree of homing and age at maturity. Much later, Parker (1964, 1965, 1968) used this method to estimate the ocean mortality rate of central B.C. pink salmon stocks. Marking of juvenile sockeye was carried out by Foerster (1936) in 1930 and 1931 as part of his well-known study of the relative efficiency of natural and artificial propagation of sockeye salmon at Cultus Lake. Another marking program on seaward migrating sockeye from Lakelse and Babine lakes of the Skeena River system was carried out from 1944 to 1948 (Aro 1951) to reveal the migration times of these stocks through the fishery, fishing rates, and the degree of homing.

In the 1960s the largest juvenile marking program of its time was carried out on chinook and coho from the Columbia River and Puget Sound. From 1962 to 1968, 39 million juveniles were marked and released (Godfrey 1971). This program was carried out by United States workers primarily to assess hatchery production, but the many recoveries throughout the coast in both United States and British Columbia fisheries proved useful in identifying migration routes and times of the stocks and the extent to which they contributed to the various fisheries.

The development of the coded microwire tag in the 1960s (Jefferts et al. 1963; Bergman et al. 1968) provided for the first time a tag which could be applied successfully to large numbers of juveniles, was readily recoverable (when in combination with an external mark), and, most importantly, provided an almost unlimited number of separate codes to identify stocks or experimental groups. In recent years, close to 8 million juvenile chinook and coho have been tagged and released each year by U.S. and Canadian agencies, involving up to 800 different stocks and treatment groups.

Age at Maturity

Two early observations of the life history of Pacific salmon bore directly on the aging studies which followed and on the application of age data to stock–recruitment relationships. The quadrennial cycle in abundance of Fraser River sockeye

suggested maturity at 4 yr of age. Observations on the spawning grounds revealed that Pacific salmon, unlike their Atlantic cousins, died after spawning (although this observation remained controversial for many years). With age at maturity known, it became possible to relate returns to the number of parents of a single brood year.

Borrowing heavily from methodology developed in Europe to determine the age of Atlantic salmon from their scale characteristics, the general life history type, and age of maturity of Pacific salmon species were established by Gilbert (1913) and Fraser (1917, 1921). Gilbert began his study of British Columbia's sockeye in 1911 and in 1912 initiated a series of annual reports on the age composition of the catch in major sockeye fisheries which were continued by various workers through to the 1970s.

The other four species have been less consistently examined. Gilbert's (1913) conclusion that pink salmon invariably mature at 2 yr of age was soon confirmed by Fraser (1921). Since then, pinks have received little attention, and that given has been mainly to see if exceptions to the 2-yr life cycle occur. Work on aging chinooks and coho was carried out in the 1920s and 1930s by Mottley (1927) and Pritchard (1940), by Milne (1964) in the 1950s, and most recently largely by Godfrey (1968), Ball (1968), and Ball and Godfrey (1967, 1968a, b, 1969, 1970).

Catch and Escapement

Records of catch by species have been kept since the early years of the fishery. Initially the numbers caught were calculated from the number of cans of salmon (the pack) put up each year at the different canneries. Prior to the widespread use of powered vessels this system worked reasonably well, since both fishing and processing were confined to locations close to the river mouths and the pack provided a useful record of the catch of stocks migrating into the rivers. With the use of power, the fleet became more mobile and was able to extend its area of operation. A fish-collecting system was established to bring fish from distant fishing grounds and to allow processors to centralize their canning facilities. As this change occurred, the pack records began to reflect the catch of a much wider mixture of stocks and became less reliable as an indication of area of capture. In 1950 and 1951, the Department of Fisheries initiated a coastwide system to record catch by area of capture. The British Columbia coast was divided into 30 statistical areas. The use of a sales slip system provided an area breakdown of catch by gear, species, number, weight, and in the case of chinook salmon, grade. This system, with minor modification to statistical areas, has remained in effect up to the present time.

The early recognition by managers of the dependency of run size on the number of parent spawners resulted in a great amount of effort expended annually in estimating the abundance of spawners to British Columbia streams. Annual spawning ground surveys became routine before the turn of the century, and up to 1956 were reported in British Columbia Provincial Fisheries Reports. Estimates of the number of spawners were almost totally subjective, with such descriptions as "satisfactory," "light," and "heavy" used. In the late 1940s, a more objective system began and each fishery officer submitted annually for each stream surveyed a form which provided estimates of the number of spawners by species in 12 size categories, ranging from less than 50 salmon to more than 100 000. This system has continued and currently escapements to over 1200 streams and rivers are reported. In addition to these routine surveys, counting fences have been operated or tag-recovery programs carried out to provide more accurate estimates of the spawning population of a particular stock or stock group.

Current Application of the Stock Concept

The large amount of information generated by the above work reinforced, in the minds of biologists and fishery managers, the stock concept as a sound basis for management, and led to the operative principle that the stocks of each river must be fished at a rate commensurate with their levels of abundance and reproductive rates. Management procedures have been developed which are consistent with this principle. Essentially five steps are involved: (1) preseason forecast of abundance; (2) establishment of escapement goals (economic and social factors often weigh heavily here); (3) formulation of fishing regulations to provide the desired division of catch and escapement; (4) re-assessment of abundance as stocks enter fisheries; and (5) in-season adjustments (weekly, daily) to fishing regulations.

These steps represent a rational application of the stock concept to salmon management, but in practice they are exceedingly difficult to apply effectively. There are three major underlying and interrelated problems: the number of different stocks involved, common or overlapping migration routes and times, and methods of harvesting the catch.

Multiplicity of Stocks

There are more than 1200 streams and rivers in British Columbia in which one or more salmon species spawn. The number of streams utilized varies according to the species but ranges from about 250 for chinook to nearly 1000 for coho. Spawning populations range in size from less than 100 salmon to more than 1 million.

Aro and Shepard (1967) described for each species the distribution and abundance levels of spawning populations in British Columbia. Although their data are from the period 1952–62, they remain reasonably representative of the current situation. Figure 1 is taken from Aro and Shepard and shows the distribution and abundance of just one species, that of chum salmon. There are close to 900 chum stocks spawning in most streams and rivers along the B.C. coast. When these are considered together with the more than 2000 of the other species, the problem of managing by stock or even by groups of stocks is clearly evident. As a further complication, Healy (1981) points out that because of the variable age of return of the five indigenous species of Pacific salmon, the fishery manager, in any one year, must also cope with adults returning from as many as 17 different brood lines.

Migration Routes and Times

Taggings both on the high seas and in coastal waters have provided a considerable amount of information on the migration routes of maturing salmon as they approach the coast

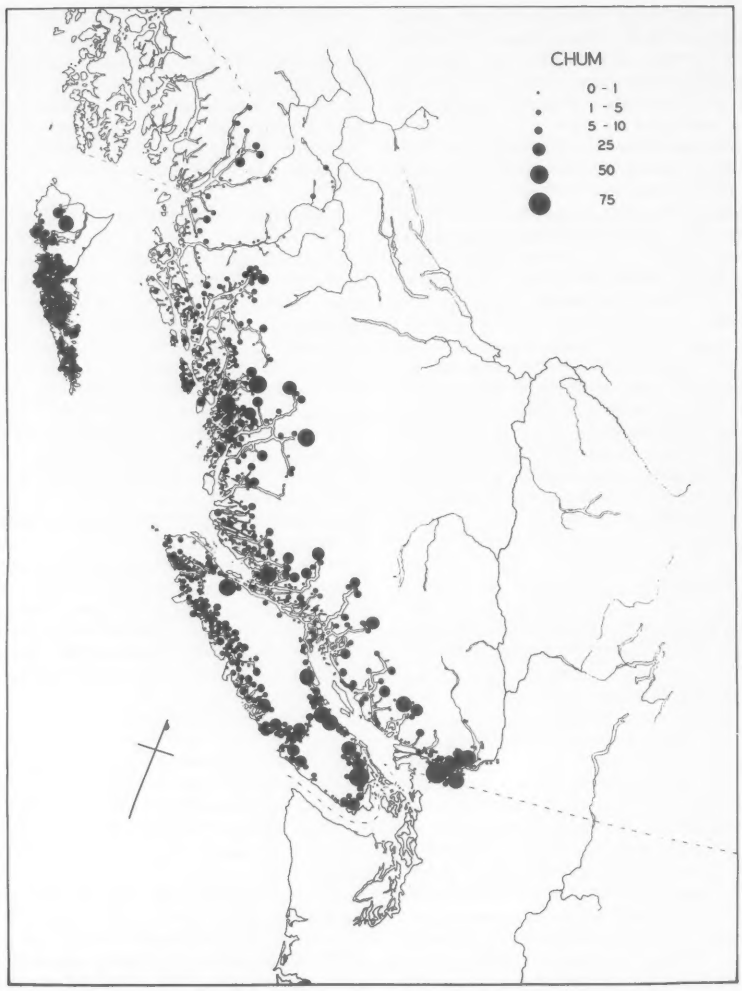

FIG. 1. Estimated average annual numbers, in thousands, of chum salmon spawners in British Columbia streams from 1951 to 1962.

and proceed to their river of origin (Milne 1957; Hourston et al. 1965; Royce et al. 1968; Godfrey et al. 1975; French et al. 1976; Neave et al. 1976; Major et al. 1978). Figure 2 illustrates the general path of the migration of the five species along British Columbia's coastline. Stocks approaching the coast generally make a "landfall" to the northwest of their river of origin and proceed southeasterly along the outer coast, peeling off from the main coastal route to enter streams along the outer coast or to proceed through straits and entrances to inside waters.

At this time, species and stocks within species are mixed extensively in the salmon fisheries along the coastal migration routes. This is evident when the timing of catches is examined (Fig. 3). Almost all the catch of sockeye, pink, and coho is made from July through September, with peak catches in August. Chums are somewhat later and chinook earlier but still one-half or more of the catch of these two species is made in the July to September period.

Within species, the migration times of individual stocks also overlap considerably. To illustrate this point I have drawn on Skeena River sockeye and pinks as examples. Skeena River sockeye are comprised of 18 major stocks (Aro and Shepard 1967), 12 of which spawn in the large Babine Lake system. Tag and recovery data have revealed the times at which some of the major spawning components are present in the Skeena River commercial fishing area (Fig. 4). Stocks

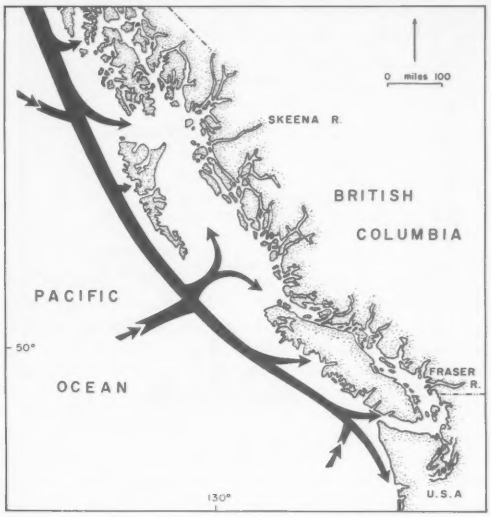

FIG. 2. General migratory path of maturing Pacific salmon along the British Columbia coast.

proceeding to spawning areas other than Babine Lake tend to be relatively early, particularly the Alastair and Lakelse lakes stocks, but nevertheless they are present in the fishery with the forerunners of stocks destined for Babine Lake. Since Babine Lake stocks are much larger (Babine stocks produce over 90% of Skeena sockeye), Babine sockeye are at least equally abundant even very early in the fishing season.

Skeena River pink salmon are abundant in the fishery from mid-July to nearly the end of August. Information on timing is available for only a relatively small number of the 73 spawning populations involved (Fig. 5), but is sufficient to demonstrate the high degree of mixing which occurs during the fishing season.

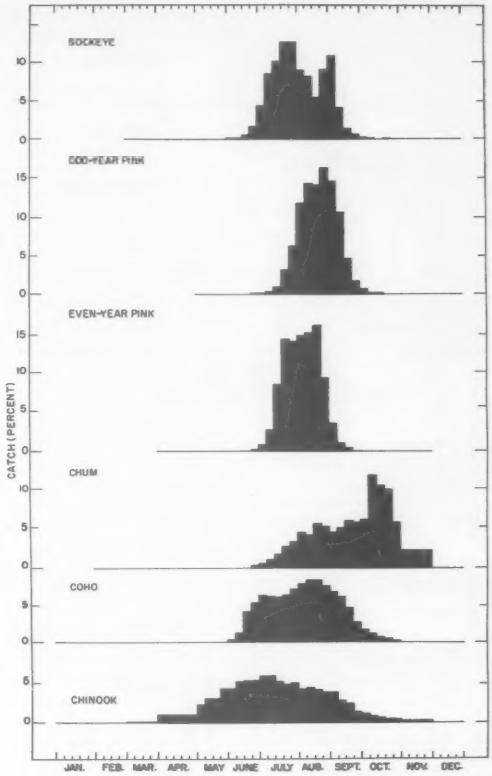

FIG. 3. Average weekly catches (expressed as percentages of the total seasonal catch) of the five species of Pacific salmon in British Columbia waters during the period 1951 to 1963. For sockeye and odd-year pinks, catches made in the United States section of the Fraser River Convention Areas have been included.

HARVESTING

There are three basic commercial gear types used in British Columbia to catch salmon: gill nets, purse seines, and trolling gear (hook and line). Traditionally, gillnet vessels have operated mainly in terminal fishing areas, i.e. in or near the river mouths or at the heads of inlets. The larger purse-seine vessels usually fish in straits or passages along salmon migration routes. The majority of the troll fleet operates in open waters and ranges as far as 50 km offshore.

Before the use of powered vessels, fishing of necessity took place in areas closely adjacent to the river mouth where shore facilities existed. Consequently, the catch in each area consisted of local identifiable stocks. The use of powered vessels resulted in a dramatic change in the fishery. It permitted development of the open ocean troll fleet and allowed net fishermen to range further from river mouths. Development of the packing system mentioned earlier, which allowed fishermen to deliver their catch on the fishing grounds, encouraged the seaward extension of fishing and at the same time the amount of actual fishing time possible by each fisherman. The availability and widespread use of synthetic nets, new lures, power gear, fish finders, and sophisticated navigational aids added substantially to the catching power of all three gear types.

Over the years, fishery managers responded in various ways to the steadily increasing mobility and catching power of the fleet. River fishing boundaries were moved seaward to reduce fishing rates by shifting effort to areas in which the fish were less concentrated. Restrictions on net length, depth, and mesh size were imposed. The number of days of fishing permitted for net fishermen each week of the season was reduced over the years from 6 d to the now common 1 or 2 d. Trollers, on the other hand, still may fish 7 d per week except in some nearshore areas, where they must observe the same fishing times as net fishermen. One of the most important measures taken in recent years was the implementation in 1969 of a license limitation scheme. While the scheme put a ceiling on the number of fishing vessels, it also allowed trans-

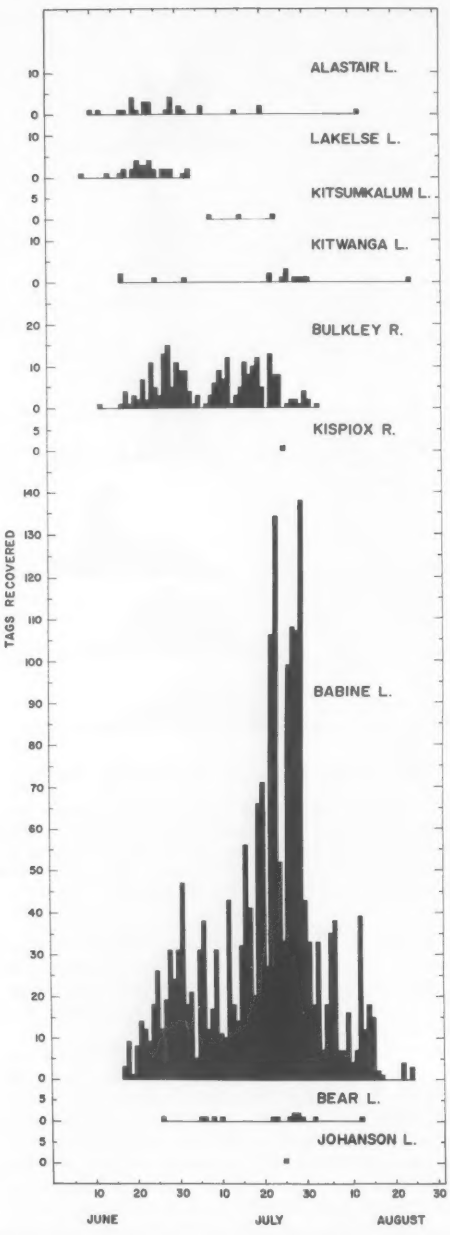

FIG. 4. Comparison of sockeye tag recoveries at various Skeena River spawning areas plotted by the dates when the fish were estimated to have passed the river boundary.

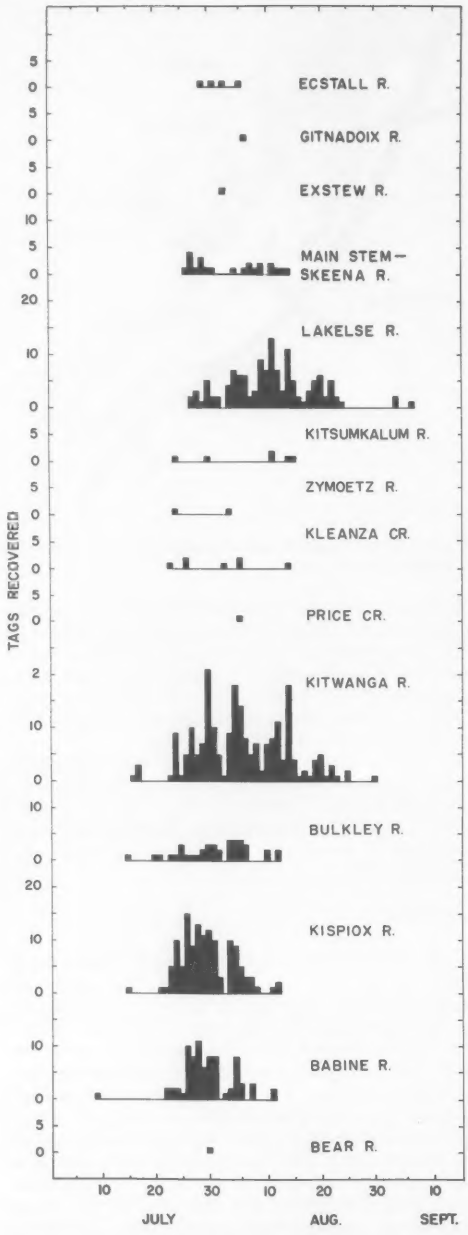

FIG. 5. Comparison of pink tag recoveries at various Skeena River spawning areas plotted by the dates when the fish were estimated to have passed the river boundary.

TABLE 1. British Columbia salmon catch (in millions) by gear type, 1951–79.

Period	Average catch all gear	Gill net		Seine		Troll	
		Avg. no.	%	Avg. no.	%	Avg. no.	%
1951–55	23.1	9.3	40	11.1	48	2.7	12
1956–60	18.3	7.6	42	7.9	43	2.8	15
1961–65	21.1	8.4	40	9.0	42	3.7	18
1966–70	24.5	9.1	37	10.3	42	5.1	21
1971–75	22.0	7.5	34	9.7	44	4.8	22
1976–79	23.4	5.9	25	11.3	48	6.2	27

fers of vessel tonnage from one gear type to another. The result has been a substantial increase in the number of seine vessels from 425 to 526 between 1970 and 1979, and a reduction in gillnet vessels from 2540 to 1332 in the same period. The number of trolling vessels and gillnet–troll combination vessels has remained relatively static at about 3000.

Regulatory actions taken over the years may have served, at least in the short term, to reduce fishing rates but did not prevent the shift of effort and catch from terminal fishing areas to areas where more extensive mixing of stocks occurs. Indeed, the early boundary changes together with the recent licence limitation scheme contributed to it. The extent to which this shift has occurred can be examined by comparing the gillnet catch (made largely in terminal fishing areas) to the catches by seine and troll (Table 1). Since the 1960–65 period, gillnet catches have decreased from about 40% of the total to 25%. The seiners' share, after dropping slightly in the 1960s, regained its former level of 48%. The proportion of the catch taken by trollers has more than doubled since 1951.

Future Prospects

The problems outlined in the previous section of this paper place severe restraints on optimal management of British Columbia salmon. The large number of stocks involved, together with intensive fishing on mixed stocks, has largely precluded the development of useful stock–recruitment relationships as a basis for forecasting abundance and for setting escapement goals. The catching power of the fleet has become so great and fishing time so short that the provision of hoped-for escapements is becoming as much good luck as good regulation.

It is difficult to be optimistic about all but the most productive stocks, if current fishing pressure and patterns continue. There are no easy solutions. Although additional biological information and further development of fishing theory for multistock fisheries will be helpful, any solution will require as its prime element drastic steps to reduce fishing effort, particularly in areas where extensive stock mixing occurs. Such steps will cause severe social and economic problems which will require difficult political solutions.

There are other possible options. We can continue as in the past with short-term solutions which create long-term problems and let the stocks and industry take the consequences. We can continue as in the past and also attempt to compensate for lost production through artificial propagation. This latter course appears to be the one being followed at the present time. The questions of license limitation and catch allocation are being examined currently, but prospects of substantial change in the fishery seem dim judging by past performance. In the meantime, the salmon enhancement program begun in 1977 continues to gain momentum.

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Significance of the Stock Concept in Artificial Propagation of Salmonids in Alaska[1]

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Hatcheries could make a significant contribution to the enhancement of salmonid fisheries if application of this technology is based on principles of the stock concept. Evidence for the stock concept is reviewed and discussed in relation to transplantation of stocks, mating procedures, maintenance of genetic diversity, different methods of artificial propagation, and location of artificial propagation facilities. A strategy is developed for management of both wild and artificially propagated stocks.

Key words: hatcheries, salmon, stock concept, genetics, artificial propagation

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Pourvu que la technologie soit fondée sur les principes du concept de stock, les écloseries peuvent apporter une importante contribution à la mise en valeur des pêches de saumons. Nous passons en revue le concept de stock et l'examinons en relation avec le peuplement, les croisements, le maintien de la diversité génétique, les différentes méthodes de propagation artificielle et l'emplacement d'installations de propagation artificielle. Nous décrivons une stratégie de gestion des stocks tant sauvages qu'artificiellement propagés.

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DURING the past 10 years, efforts to promote and build salmon hatcheries in Alaska have accelerated greatly, largely as a result of advances in incubation technology of pink salmon and chum salmon (Bams 1970). Responding to requests by various groups for application of this technology, the Alaska Legislature passed Alaska Statute 16.10.400 which authorizes the operation of private, nonprofit hatcheries for salmon. Reacting to the lack of genetic considerations in this statute, the Alaska District of the American Institute of Fishery Research Biologists issued a position paper on genetics and hatcheries (American Institute of Fishery Research Biologists 1975). Genetic hazards of extensive transplanting of stocks were a major emphasis of this paper.

The validity of the stock concept in salmonids has been recognized and reconfirmed for more than 40 years, but this concept has not been integrated into the design of most salmonid culture activities. Many fishery scientists have discussed the benefits to be gained by application of the stock concept and basic genetics to salmonid culture practices, e.g. Calaprice (1969, 1970); Simon (1970, 1972); Behnke (1972, 1979); Bams (1972, 1976b, 1979); Lannan (1973); McIntyre (1975); Reisenbichler and McIntyre (1977); Wagner (1979). The objective of this paper is to review briefly the concept of stocks and the genetics involved in relation to some recently published data and to present a strategy for application of the stock concept in artificial propagation of salmonids, especially in Alaska.

Adaptation and the Stock Concept

Stocks[2] of salmon and trout exist because of adaptation to local environments and the marked ability of these fish to "home" — progeny tend to return to their natal streams or lakes to spawn. This ability of salmonids to home is well documented, e.g. Davidson (1934); Scheer (1939); Pritchard (1939); Rich (1939); Shapovalov (1941); Cope (1957); Lindsey et al. (1959); Hartman and Raleigh (1964); Parker (1964); Hasler (1966); Bams (1972); Ricker (1972); Armstrong (1974); Bailey et al. (1976).

Many river, lake, or stream systems contain more than one stock of salmon or trout of the same species. After many

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[2]The term "stock" refers to "the fish spawning in a particular lake or stream (or portion of it) at a particular season, which fish to a substantial degree do not interbreed with any group spawning in a different place, or in the same place at a different season" (Ricker 1972, p. 28).

generations of natural selection, each stock becomes uniquely adapted to the particular environments experienced during its life history. This adaptation to the local environment is the result of selection of optimal genotypes. Gene combinations that are best suited for the survival of each stock prevail.

Recognition of local stocks of salmon was strongly supported by Rich (1939, p. 47), "To summarize: Diverse evidence points so clearly to the existence of local, self-perpetuating populations in the Pacific salmon that any hypotheses that do not conform must be subject to considerable doubt." Since 1939, much additional evidence has demonstrated adaptation of salmon and trout to specific environments. Ricker (1972) provides one of the most extensive documentations of this evidence.

Specific examples from this literature demonstrate the complexities of adaptations to local environments. Rainbow trout (*Salmo gairdneri*) residing in a stream above and below a waterfall differed in meristic characters and biochemical genetic diversity (Northcote et al. 1970). In Pacific salmon, time of spawning often represents genetic adaptation to specific environments (see Calaprice 1969; Ricker 1972). Pink salmon (*Oncorhynchus gorbuscha*) at Olsen Creek, a small coastal stream in Prince William Sound, Alaska, consistently return in a predictable pattern to specific areas of the stream at specific times (Helle et al. 1964; Helle 1966, 1970; Thorsteinson et al. 1971). Returns of marked pink salmon to Auke Creek (near Juneau, Alaska) clearly demonstrated that early and late spawners produce progeny that spawn at the same season as their parents (Taylor 1980). Arctic char (*Salvelinus alpinus*) have been shown to home with a high degree of precision to feeding and spawning sites in the Wood River Lake system in western Alaska (McBride 1980). These consistent behavioral patterns are strong evidence for adaptation to local environments. Early migratory behavior of some stocks of juvenile salmon and trout has been shown to be an adaptation to local environments. The progeny of sockeye salmon (*Oncorhynchus nerka*) that spawn in lake outlets migrate upstream to reach the lake to rear, whereas the progeny of fish spawning in tributaries to the lake simply migrate downstream to reach the lake. These behavioral responses have been shown to be largely under genetic control (Brannon 1967; Raleigh 1967).

The migratory responses of sockeye salmon fry in multiple lake systems of the Fraser River in British Columbia, Canada, were evaluated by Brannon (1972). The fry in six stocks he examined required distinctly different migratory responses to reach their nursery lakes. Hybridization experiments demonstrated that the early migratory behavior in these stocks has a strong genetic basis.

Direction of early migration of fry of rainbow trout and cutthroat trout (*Salmo clarki*) that spawn in outlet and inlet streams of lakes has also been shown to be largely under genetic control (Raleigh 1971; Raleigh and Chapman 1971; Bowler 1975). Many other examples exist that document behavioral, physiological, and morphological adaptation to local environments in salmonids, e.g. Bams (1969), Ricker (1972), Altukhov (1974), Konovalov (1975), Koski (1975), Behnke (1979), Rosly (1981). The specifics of these adaptations can be highly complex. Can these adaptations be lost or diluted by intraspecific hybridization with transplanted stocks? Does artificial propagation affect these adaptations?

Transplantation of Stocks

Man has transplanted animals (and plants) from one area to another for many years for many different reasons. This practice has some disturbing biological implications that are seldom acknowledged. A quotation from Mayr (1971, p. 196–197) concisely states the problem:

"One conclusion emerged from these observations more strongly than any other: the phenotype of every local population is very precisely adjusted to the exacting requirements of the local environment. This adjustment is the result of a selection of genes producing an optimal phenotype. The discovery of this physiological adaptation of local populations is of considerable practical importance for instance in wildlife management. Populations that are well-adapted in their native environments are often very vulnerable when transplanted into different environments. The literature on game animals records many instances in which stock died out rapidly after introduction into a different region. *If they survive long enough to breed, introgression of their inferior genes will contribute to the deterioration of the native stock.* (Emphasis added.)

It is for this reason some countries now prohibit the import of game birds and mammals. Millions of dollars of taxpayers' money spent on raising and releasing ill-adapted game stocks could have been saved if those in charge had been aware of the physiological differences among local populations."

Even though Mayr was specifically referring to game animals, the genetic principles involved apply equally to fish. Records of transplanting stocks of salmon show no lack of imagination on the part of the transporters. Shipments of eggs or juveniles of chinook salmon (*Oncorhynchus tshawytscha*) during the period 1872–1930 were sent to 17 states east of the Mississippi River and to countries like Tasmania, Nicaragua, Italy, Mexico, Argentina, and Germany (Davidson and Hutchinson 1938). Chinook salmon were even transplanted, unsuccessfully, to Hawaii on several occasions.

Biologically, salmonid transplants can be categorized in three ways: (1) Range extension — transplant of a species to an area where that species is not present. (2) Reintroduction — transplant of a species to a barren system in an area where the species exists in nearby systems. (3) Supplementation — transplant of a species to a system where that species is already present. Range extension presents more of an ecological problem than a genetic problem. The transplant of coho salmon (*Oncorhynchus kisutch*) to the Great Lakes is an example (Tody 1966). There were no natural coho salmon populations in the Great Lakes, so interbreeding was not a problem. Reintroduction and supplementation present the genetic problems.

Homing of transplanted stocks of salmon has been highly variable (Worlund et al. 1969; Ricker 1972; Simon 1972), but the primary objective of most studies has seldom been to evaluate homing behavior of transplanted stocks. Exceptions are the comprehensive experiments done by Bams (1972, 1974, 1976a, 1979). He conclusively demonstrated that homing ability of transplanted pink salmon was not precise and that by hybridizing the transplanted stock and the indi-

genous stock, the homing ability was improved by a factor of 10 (Bams 1972). Bams' experiments strongly support the hypothesis that homing ability is associated with genetic adaptation to specific environments.

The imprecise homing ability of transplanted stocks increases the chances they will stray to other rivers or streams and interbreed with wild fish. The extent to which this interbreeding would be detrimental to the adapted wild stock depends on the relative numbers of fish involved. The importance of the adaptation of an animal to its particular environment and how genetic changes may reduce fitness is stated by Strickberger (1968, p. 778–779):

"In general, genetic homeostasis depends upon the array of gene frequencies built up by a population over the long period of its evolution in a particular environment. Since these established gene frequencies have been selected to confer a high degree of fitness upon a population, any rapid departure from these frequencies may be expected to reduce fitness."

The potential for endangering gene combinations of proven adaptive value by hybridization (intraspecies) is clearly discussed by Dobzhansky (1951, p. 179–253). Damage to genetic adaptiveness of our native salmon and trout stocks by intraspecific hybridization is difficult to assess because smaller-than-expected returns could be blamed on overfishing or unfavorable environmental conditions.

Certainly, there have been "successful" transplants of salmon and trout, and these results are readily located in the literature, e.g. Meehan (1966), Ellis (1969), McNeil et al. (1969), Jensen and Duncan (1971), Blackett (1979). Not so readily located in the literature are descriptions of the enormous numbers of "unsuccessful" transplants. Unsuccessful experiments are seldom reported in the literature, and the data are most often left in the files.

Differences Between Agricultural Genetics and Aquacultural Genetics

In agricultural situations where man controls the breeding of animals and plants, selection for emphasis of certain characteristics is commonly practiced. Artificial selection reduces genetic variability. Recent examples in food crops illustrate the extent to which genetic uniformity from intense selection results in uniform susceptibility to natural disasters like new strains of disease organisms (Harlan 1972; Wade 1972). The solution to these problems is clearer for plants than for animals. First, the severity of the problem has to be acknowledged (Harlan 1975). Next, seeds can be stored so that wild types with a high degree of variability can be preserved in "gene banks." As we trend toward more use of "aquaculture" in our fishery resources, a similar loss of genetic diversity will occur, but the solution to this problem has to be quite different. Sperm from salmonid fishes may be cryopreserved for a short time (Ott and Horton 1971), but no similar technique has been developed for ova.

Two basically different systems of aquaculture are currently used: (1) confined systems (intensive culture), and (2) unconfined systems (extensive culture). The genetic strategies needed are very different for each. If fish are to be confined in raceways, ponds, or closed systems during all their lives (category 1), then many of the breeding schemes developed in agricultural genetics will be useful. Selective breeding, development of inbred lines, and heterosis (hybrid vigor) are familiar methods and goals in agricultural genetics (Brewbaker 1964). The application of these techniques and others in aquaculture ventures is discussed by Calaprice (1970), Simon (1970), and Purdom (1972). If, however, fish are released in streams, lakes, or oceans to survive natural environmental fluctuations and compete for space and food with wild populations, then use of genetic tools like selective breeding and inbreeding could be counterproductive.

Clearly, the greater the adaptive (or stock-specific) genetic variability present in a stock, the greater are the chances that the stock will be able to respond positively to environmental changes. In addition, the ability to adapt to local fluctuating environments would logically require that a stock has a high degree of adaptive genetic diversity. Breeding schemes involving artificial selection or inbreeding reduce genetic diversity. Pleiotropic effects associated with artificial selection can further reduce genetic diversity (Dobzhansky 1970; Strickberger 1968). Obviously, breeding schemes that maintain or enhance adaptive genetic variability will be advantageous to a stock of salmon released to compete in the ocean.

Effects of Courtship and Spawning Behavior on Genetic Diversity of Stocks

Perhaps the question of how to make matings in a salmon hatchery could be answered if we better understood how matings are accomplished naturally in wild populations. Observations I made on courtship and spawning behavior of pink and chum salmon (*Oncorhynchus keta*) at Olsen Creek, in Prince William Sound, Alaska, between 1958 and 1975, indicate the need for use of more males in breeding schemes for hatcheries. I made these observations under water using two techniques: (1) lying on the stream bottom dressed in a neoprene wetsuit with mask and snorkel (see National Geographic, August 1968, p. 218) and (2) sitting in the stream (wearing a wetsuit) and watching the activity of the fish through a 35-mm reflex camera with a telephoto lens and magnified waist-level viewfinder placed in a waterproof open-top case.

Concomitant with the construction of the redd by the female, a hierarchial order of one dominant and one to five or more subordinate males develops around the female. The rank is determined by fighting. The dominant male performs most of the courtship displays with the female. Moving back and forth over her caudal peduncle is one such display. This activity also keeps the subordinate males to the rear of the redd where they interact with each other for rank.

When the female is close to being ready to spawn, her interactions with other females change. She stops initiating attacks on nearby females and responds very passively to attacks by other females of her own or another species. At the same time, the subordinate males become more active and the dominant male has trouble keeping them at the downstream edge of the redd. When the female is ready to spawn, she lies in the redd with her head facing upstream and her vent in the deepest portion of the excavation. She starts to gape her mouth, and immediately the dominant male takes a position beside her. The other males swim into the redd, and one takes a position beside the female on the opposite side, and the other males take up positions beside the dominant male on one side

of her and beside each other on the opposite side. With mouths agape, the female releases the eggs, and the males release the milt simultaneously. The water in the redd turns cloudy from the white milt, and several seconds go by before the milt starts to spill over the rear lip of the redd. Then the female starts her fanning or digging flexures in rapid sequence just ahead of the upstream lip of the redd. After she finishes a series of flexures, she quickly circles back and starts another series. This action fans out gravel which settles in the redd and covers the eggs. At the same time, the female is starting the excavation of a new redd. Her rate of fanning gradually decreases to a slower pace.

Meanwhile, the group of males she has spawned with usually desert her and may try to enter the hierarchy of males around other nearby females. By the time the female is ready to spawn again, she may have a completely new hierarchy of males around her although some of the original males may remain.

The number of redds a female constructs likely varies in relation to many factors, e.g. floods and density of spawners. Considering that at Olsen Creek the average stream life of a female is about 11 d and the fecundity of pink and chum salmon females is about 2000 and 3000 eggs, respectively, and each orgasm lasts about 10 s; it seems likely that each female could spawn from three to five times or more. If a female spawned five times with 5 different males each time, 25 males would have fertilized her eggs! This would be an extreme case. Regardless, the important point here is that the eggs of each female are fertilized by many males, each with different genetic composition. Often in production hatcheries, one male is used to fertilize several females.

The spawning behavior in pink and chum salmon ensures that future generations maintain a high degree of adaptive genetic variability. Spawning of each female with several males is an especially advantageous strategy for pink salmon because they invariably mature at 2 yr of age. In contrast, in salmon other than pink salmon, several year-classes may spawn together, which results in combining the adaptive genetic diversity from several brood years.

Fertilizing the eggs of each female with several males would be very prudent in a hatchery operation. A sex ratio of 1:1 seems minimal when compared with the sex ratio of observed natural matings.

Effects of Artificial Propagation on Genetic Composition of Stocks

Wild populations of salmon maintain adaptive genetic diversity through natural selection including their spawning behavior. Any form of artificial propagation that increases survival by reduction of natural mortality at any life history stage will change the genetic composition of the original stock. Genetic change (change in gene frequency) can be introduced into a stock by artificially mixing eggs and sperm. Selection of gametes from only large fish or early maturing individuals will, of course, reduce genetic diversity; but artificial matings made at random may also introduce change. Natural matings of salmon are variable, and partners are determined through complex courtship behavior and establishment of hierarchies. The eggs from one female are fertilized by many different males. Until we understand the genetic significance of natural spawning behavior, our only hope for maintaining genetic diversity in the hatchery situation is by use of the eggs and milt from randomly picked individuals representing the gene pool of the total stock.

The most obvious situation for introducing genetic change in a stock is in salmon hatcheries where young are raised to the smolt stage. Here we release fish that have undergone no natural selection for fitness in the wild freshwater environment. Certainly the progeny of these fish will eventually be genetically different from "wild" individuals of the same stock. If the hatchery-produced smolts return to the hatchery as adults, one would expect rapid selection for an optimal "hatchery-type" fish.

Based on the above considerations, different methods of artificial propagation can be evaluated for their likelihood to introduce genetic change or to maintain genetic diversity. Artificial spawning channels would introduce the least genetic change because the fish make their own matings, and usually no artificial rearing is involved. Incubation channels and hatcheries for pink salmon and chum salmon would be next best because they require little or no rearing of fish beyond the fry stage. Hatcheries in which fish must be raised for a long period beyond the fry stage, mainly those for chinook salmon, coho salmon, and steelhead trout, create the greatest potential for genetic change. The smolts released from these hatcheries have undergone no natural selection in the stream environment; therefore, selection favoring an optimal "hatchery-type" fish should occur.

Can Hatchery and Wild Stocks Coexist?

The potential genetic effects of superimposing hatchery fish on wild stocks of the same species depend on the species, the method of artificial propagation, and the situation. Pink salmon are restricted to a 2-yr life cycle, so deleterious effects of interbreeding cannot be exchanged between year lines. All of the other salmon have multiple-age-classes, so genetic change occurring in 1 brood year will eventually affect all brood years. Nonadaptive genes introduced into the gene pool by interbreeding could be perpetuated for many generations as recessives (Mayr 1971).

As a hypothetical example, say a hatchery were built on a small pink salmon stream and the indigenous stock was used in the hatchery and also allowed to spawn naturally in the stream. Because of the higher survival in the hatchery, the run would eventually be dominated by the returns from the hatchery releases. If the stream were situated so that the returns could be harvested separately from other stocks, it could be a manageable system. If the returns were harvested while mixed with other stocks and the hatchery fish could not be identified in the catch, then it would be an unmanageable situation. If an outside stock were brought into the hatchery in place of, or in addition to, the indigenous stock, the genetic patterns of the locally adapted indigenous stock would be altered by interbreeding, and fitness of both the wild and hatchery stocks would suffer. Additionally, the homing ability might be altered; and if the survivors strayed to nearby systems, the gene pool of the locally adapted stocks in these systems would be altered by introgression.

If the hatchery were built on a barren system, a transplanted stock would have to be brought in; then imprecise homing

would become the major problem. Are we willing to jeopardize other stocks of fish in the area?

Another consideration would be the number of stocks in a system. The more stocks, the greater the problem. If we enhanced one stock in such a system, could we harvest the greater returns without overfishing the other stocks? Timing and identification of the runs is of obvious importance in this situation.

What if we had built a successful hatchery for a species such as coho salmon, chinook salmon, or steelhead trout instead of pink salmon? Here the wild stock would eventually suffer, not only because of differences in exploitation rates that would have disadvantaged the wild stock, but also because the hatchery stock would not be submitted to natural selection as juveniles in the stream thereby reducing the fitness of naturally spawning fish that were offspring of crosses between wild fish and hatchery-produced fish. In this situation, we would eventually be committed totally to the hatchery for our desired production levels. This type of hatchery is necessary in some situations, but some difficult and probably permanent decisions have to be made in the early planning stages. Recent hatcheries of this type, where the stock concept has been rigidly integrated into the design, have been very successful (Heard and Crone 1976; Reimers 1979).

Another hypothetical hatchery situation could be one in which we planned to use the hatchery stock as a source of eggs or smolts to develop other hatcheries or enhancement programs. Development of a hatchery of this type for planting fish in a "closed" system or for a "put-and-take" fishery in a closed system is certainly desirable. For general use in projects involving anadromous fish in Alaska, this situation would be biologically dangerous. We would endanger already depleted stocks of salmon with the hazards of transplantation and loss of genetic diversity on a large scale. The wide dissemination of a generalized stock would constitute a genetic impediment that could reduce fitness of a great many stocks. We should not consider this type of hatchery operation.

Strategy for Successful Management of both Wild and Artificially Produced Stocks of Salmonids

Our primary goal in management of our salmonid resources should be to maintain as many viable diverse wild stocks as possible. When we intend to augment the numbers of fish available to a fishery with hatchery technology, there are some precautions. Hatcheries have been promoted without adequate consideration of the problems they may create. Hatcheries are not a panacea (Narver 1973). Rhetoric about the benefits of hatcheries should not make us complacent about our natural streams, rivers, lakes, and oceans. These diverse environments provide us with diverse stocks of salmonids. Our natural watersheds are our "gene backs" for salmonid fishes.

Recognition of key watersheds as gene banks in Alaska was recommended by the American Institute of Fishery Research Biologists, Alaska District (1975). Most of the anadromous fish streams and rivers in Alaska are still relatively unchanged by man. This fortunate circumstance will be increasingly threatened as uses noncompatible with anadromous fish production for our rivers develop, e.g. hydroelectric dams. We need to identify and recognize many of our unique watersheds as "gene banks." These special watersheds should be protected from uses that would be noncompatible (artificial propagation or hatchery facilities included) with natural production of the indigenous fish stocks.

Each species and stock of salmon and trout has special requirements, and categorizing all potential watersheds for gene bank status will be difficult. However, the characteristics of certain unique stocks and watersheds are well known and should be recognized immediately.

Supplementation of stocks can be accomplished in several ways. Artificial spawning channels have proven to be enormously successful for sockeye salmon (*O. nerka*), chum salmon (*O. keta*), and pink salmon (*O. gorbuscha*) in Canada (Cooper 1977; Mead and Woodall 1968). More consideration should be given to this technology in Alaska. Spawning channels have a decided advantage over conventional hatcheries in reducing potential genetic problems associated with artificial mating.

When hatchery technology is the preferred method of supplementing natural production of specific stocks, certain considerations are essential to ensure success. First, transplantation of stocks should be avoided. Second, the requirements of stocks at various life history stages must be known. The hatchery or other enhancement facility is then adapted to the needs of the fish (and not vice versa). Third, knowledge of the timing and path of returns is essential to manage the harvest. Fourth, location of the hatcheries will be the most important factor in determining the success of maintaining wild and artificially produced stocks in a general area. Returns to artificial propagation facilities have to be separable in time or space from local wild stocks, or the system will be unmanageable. Our record for successful management of mixed-stock salmonid fisheries is poor. To superimpose a new stock with a different exploitation rate into a mixed-stock fishery would exacerbate the management problem, and the wild stocks will suffer.

The future of our salmonid resources can be bright indeed if we adhere to the stock concept and scientific methods in the management of our fisheries.

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Comparative Survival and Growth of Planted Wild, Hybrid, and Domestic Strains of Brook Trout (*Salvelinus fontinalis*) in Ontario Lakes[1,2]

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FRASER, J. M. 1981. Comparative survival and growth of planted wild, hybrid, and domestic strains of brook trout (*Salvelinus fontinalis*) in Ontario lakes. Can. J. Fish. Aquat. Sci. 38: 1672–1684.

Matched plantings of domestic strain and interstrain hybrid (or wild strain) brook trout (*Salvelinus fontinalis*) were made annually in nine small Precambrian Shield lakes during 1973–77. Recoveries of planted fish were made by gillnetting and/or angling during 1974–80. In six study lakes, hybrids (and wild strains) were recovered at rates two to four times greater than the domestic strain; in three lakes recoveries were similar. Most domestic strain trout were caught in the year following planting whereas recoveries of hybrids and wild strains were spread over 3–4 yr. Each kilogram of hybrid (or wild) planted yielded 5.6 kg (1.2–12.3); each kilogram of domestic strain planted yielded 0.8 kg (0.2–2.1). Lakes containing only minnows and sticklebacks yielded the highest returns of brook trout; lakes containing competitive species yielded low returns. Rapid growth of brook trout occurred in lakes containing only minnows and sticklebacks; slowest growth was noted in lakes supporting white suckers (*Catostomus commersoni*). Domestic strain brook trout and the matched hybrid grew at approximately the same rate within a lake and in seven of the nine lakes ate the same food. The performance of the Nipigon × domestic hybrid qualifies it for consideration as a replacement for the domestic brook trout presently planted in Ontario lakes.

Key words: planting, brook trout, trout strain, hybrid, Precambrian Shield, survival, stock

FRASER, J. M. 1981. Comparative survival and growth of planted wild, hybrid, and domestic strains of brook trout (*Salvelinus fontinalis*) in Ontario lakes. Can. J. Fish. Aquat. Sci. 38: 1672–1684.

Des ensemencements appariés d'une lignée domestique et d'un hybride interligné (ou lignée sauvage) d'ombles de fontaine (*Salvelinus fontinalis*) ont été effectués annuellement dans neuf petits lacs du Bouclier précambrien entre 1973 et 1977. Les poissons introduits ont été recapturés par filets maillants et (ou) pêche à la ligne entre 1974 et 1980. Dans six des lacs étudiés, l'hybride (et lignée sauvage) ont été recapturés à des taux deux à quatre fois plus grands que la lignée domestique; dans trois lacs, les recaptures ont été identiques. La plupart des ombles de fontaine de lignée domestique ont été capturés dans l'année suivant l'introduction, tandis que les recaptures d'hybride et de lignée sauvage s'étalèrent sur une période de 3–4 ans. Chaque kilogramme d'hybride (ou sauvage) ensemencé donna un rendement de 5,6 kg (1,2–12,3); chaque kilogramme de lignée domestique ensemencé donna un rendement de 0,8 kg (0,2–2,1). Les lacs qui ne contenaient que des ménés et des épinoches eurent les recaptures les plus élevées; ceux contenant des espèces compétitives donnèrent de faibles retours. La croissance des ombles de fontaine dans les lacs ne contenant que des ménés et des épinoches fut rapide; la croissance la plus lente a été observée dans les lacs contenant des meuniers noirs (*Catostomus commersoni*). Les ombles de fontaine de lignée domestique et l'hybride apparié crûrent à peu près au même taux dans un même lac et, dans sept des neuf lacs, consommèrent la même nourriture. La performance de l'hybride Nipigon × domestique est telle qu'on devrait le considérer comme remplacement dans les peuplements d'ombles de fontaine présentement effectués dans les lacs de l'Ontario.

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POOR survival of domestic strains of trout, following release in the wild, has been noted and investigated throughout North America (Greene 1952; Miller 1952; Smith 1957; Vincent 1960; Flick and Webster 1964, 1976; Mason et al. 1967; Cordone and Nicola 1970). The general conclusion of these investigations has been that generations of inbreeding in the hatchery have led to a loss of wildness and to an inability of the domestic stocks to adapt to ecological conditions in the wild. This situation holds for the domestic strain of brook trout (*Salvelinus fontinalis*) routinely released in Ontario waters (Fraser 1972, 1980).

Two wild strains of brook trout (Lake Nipigon, Dickson Lake) were investigated as possible replacements for the Ontario domestic strain. Preliminary studies indicated that first-generation progeny of both wild strains grew very slowly in the hatchery and, consequently, emphasis was shifted to rearing and appraising semiwild hybrids (Nipigon × domestic, Dickson × domestic) as possible replacements for the domestic strain. Smaller numbers of the wild strains have been included in the assessment.

The procedure has been to rear interstrain hybrids under identical conditions with domestic brook trout and to plant equal numbers of one hybrid and the domestic strain in a common body of water. The study spans 5 yr of matched plantings of fall fingerlings in nine small Precambrian Shield lakes located in Algonquin Park, Ontario. Planted fish were recovered by angling and/or intensive gillnetting during 1974–80. This paper presents the results of the comparative tests.

Materials and Methods

TROUT STRAINS

The domestic brook trout stocked in most Ontario waters are the progeny of some 20 generations of domestication at Hill's Lake Hatchery in Ontario and an unknown number of generations in Pennsylvania. It is known to have had one infusion of genes from a wild strain of brook trout. In 1965 and 1966, the entire egg collections at Hill's Lake Hatchery

TABLE 1. Characteristics of study lakes.

	Group 1				Group 2			Group 3	
	Little Mykiss	Shallnot	Chipmunk	Rumley	Little Minnow	Presto	Oram	Major	Mykiss
Area (ha)	9.3	9.3	27.1	18.1	8.9	15.5	27.1	26.3	23.5
Maximum depth (m)	6.7	7.3	16.8	10.1	14.3	35.7	18.3	14.6	11.3
Mean depth (m)	2.7	3.0	6.0	3.0	5.2	14.8	5.2	7.3	5.3
Secchi disc (m)	2.1	3.7	4.3	3.5	3.5	5.5	4.4	4.8	4.8
Total dissolved solid (mg/L)	47	32	41	39	44	34	42	54	40
Total alkalinity (mg/L)	9	8	7	—	9	8	13	15	8
pH	6.2	6.4	6.7	7.0	6.2	6.9	6.7	7.0	6.5
Angling prohibited	×	×	×	×		×			×
Fish species present									
Brook trout[a] (*Salvelinus fontinalis*)	×	×	×	×	×	×	×	×	×
Splake[a] (*Salvelinus namaycush* × *S. fontinalis*)		×	×	×		×	×	×	
Golden shiner (*Notemigonus crysoleucas*)		×		×	×				
Common shiner (*Notropis cornutus*)				×		×		×	
Northern redbelly dace (*Phoxinus eos*)	×	×	×	×			×	×	×
Creek chub (*Semotilus atromaculatus*)		×	×	×	×	×		×	×
Pearl dace (*Semotilus margarita*)			×	×	×	×		×	×
Fathead minnow (*Pimephales promelas*)								×	×
White sucker (*Catostomus commersoni*)			×			×		×	×[b]
Brown bullhead (*Ictalurus nebulosus*)				×		×	×		
Pumpkinseed (*Lepomis gibbosus*)				×		×	×		
Yellow perch (*Perca flavescens*)				×	×	×			
Brook stickleback (*Culaea inconstans*)					×	×		×	

[a]Planted stock; splake are survivors from earlier plantings.
[b]Sparse population.

were fertilized by sperm from male brook trout which were F_1 progeny of a Hill's Lake Hatchery domestic female brook trout × wild Lake Nipigon male brook trout cross.

Two pure wild strains (Lake Nipigon, Dickson Lake) were selected for comparison with the domestic strain. The Lake Nipigon brook trout is long-lived (6−7 yr) and reaches a large size (world record of 6.58 kg) in a complex fish community. Fertilized eggs were obtained from two localities in Lake Nipigon, West Bay and South Bay. The Dickson Lake strain is representative of the native brook trout inhabiting Algonquin Park lakes. Lake trout (*Salvelinus namaycush*) and yellow perch (*Perca flavescens*) also commonly inhabit these lakes, and the yellow perch are heavily utilized as food by the two salmonids. Dickson Lake brook trout live 5−6 yr and may weigh 1−1.5 kg.

Three hybrid crosses were made as follows: NIP × DOM (Nipigon female × domestic male), DICK × DOM (Dickson female × domestic male), DICK × NIP (Dickson female × Nipigon male). Progeny of the first two crosses have been tested extensively in matched plantings with the domestic strain.

Study Lakes

The nine study lakes are located in the southeast sector of Algonquin Park, Ontario, at approximately 45°40′N and 78°10′W. They range from 8.9 to 27.1 ha in area and from 6.7 to 35.7 m in maximum depth (Table 1). Their waters are relatively infertile (total dissolved solids 32−54 mg/L), slightly acid (pH 6.2−7.0), and poorly buffered (total alkalinity 7−15 mg/L). The lakes stratify thermally and, although some decrease in dissolved oxygen occurs in the bottom waters of all lakes in both summer and winter, there is always sufficient oxygen for trout in the upper layers.

Table 2. Recoveries by gillnetting of planted brook trout from four study lakes (in the order domestic and Nipigon × domestic hybrid). Values in parentheses below the year of planting are mean weights in grams at planting. Gillnetting effort is in parenthesis after lake name.

	Year of planting					
	1973	1974	1975	1976	1977	Mean
Domestic	(10.8)	(9.7)	(9.3)	(16.8)	(25.2)	(14.4)
Nipigon × domestic	(6.5)	(5.7)	(7.8)	(5.3)	(6.6)	(6.4)
	Little Mykiss Lake (88 m · ha^{-1} · yr^{-1})					
Number planted per hectare	75	75	75	75	75	
	75	79	81	75	75	
Percent recovered	2.3	1.7	11.0	18.3	4.0	7.4
	3.1	6.1	23.1	25.0	16.3	14.7
Weight planted (kg)	7.6	6.8	6.5	11.8	17.6	
	4.6	4.2	5.9	3.7	4.6	
Weight caught/weight planted	1.8	0.4	3.3	4.6	0.6	2.1
	5.8	5.1	12.1	26.6	11.9	12.3
	Shallnot Lake (88 m · ha^{-1} · yr^{-1})					
Number planted per hectare	75	75	75	75	75	
	75	75	75	75	75	
Percent recovered	3.1	1.7	1.7	2.4	1.9	2.2
	5.3	10.1	18.1	11.1	5.1	9.9
Weight planted (kg)	7.6	5.6[a]	9.1[a]	11.8	17.1	
	2.1	8.3	12.7	2.4	4.6	
Weight caught/weight planted	0.8	1.0	0.6	0.4	0.2	0.6
	10.7	4.0	6.2	20.8	3.7	9.1
	Chipmunk Lake (41 m · ha^{-1} · yr^{-1})					
Number planted per hectare	45	73	59	59	59	
	69	66	55	59	59	
Percent recovered	2.4	0.7	2.9	6.3	2.7	3.0
	4.8	6.6	8.9	6.9	7.4	6.9
Weight planted (kg)	13.2	19.2	13.3	26.9	40.3	
	10.4	10.3	4.9	8.5	10.6	
Weight caught/weight planted	0.5	0.2	0.9	0.8	0.4	0.6
	0.9	3.5	11.8	4.0	5.2	5.1
	Rumley Lake (61 m · ha^{-1} · yr^{-1})					
Number planted per hectare	50	50	50	50	39	
	44	50	55	50	50	
Percent recovered	1.3	0.9	2.2	0.9	0.3	1.1
	2.0	3.3	4.7	3.1	3.3	3.3
Weight planted (kg)	9.8	8.7	8.4	15.1	17.6	
	5.2	5.1	7.8	4.8	5.9	
Weight caught/weight planted	0.3	0.3	1.0	0.2	0.0	0.4
	1.3	3.5	3.4	3.8	3.3	3.1

[a]Mean weights of these domestic lots slightly different from those noted above.

The lakes vary in their fish species composition (Table 1) and provide a wide range in potential competition for planted trout. None of the lakes contain native trout, but planted brook trout have spawned in Shallnot and Mykiss lakes with poor results. Cyprinids (one to five species) were present in all study lakes. The white sucker (*Catostomus commersoni*), the only species caught in numbers in the gill nets, was abundant in Chipmunk and Major lakes, common in Presto Lake, and scarce in Mykiss Lake. During the gillnet sampling period (1974–80), mean annual yields of white suckers were 2.6, 4.9, and 0.4 kg/ha, respectively, from Chipmunk, Major, and Presto lakes. Yellow perch were abundant in Little Minnow Lake (standing stock of 20–30 kg/ha (Fraser 1978)) and Rumley Lake, but sparse in Presto Lake. Pumpkinseed (*Lepomis gibbosus*) were numerous in Rumley and Oram lakes but sparse in Presto Lake. Earlier studies (Fraser 1981) have indicated that the standing stocks of fishes in similar lakes on the Precambrian Shield are in the order of 35–50 kg/ha.

Rearing and Planting

Domestic strain brook trout were reared at the Pembroke Hatchery from eyed eggs produced at the Hill's Lake Hatchery. Earlier experience at Pembroke indicated that growth of the wild strains and the hybrids would be much slower than growth of the domestic strain. Therefore, in 1973–75, growth of the domestic strain in one raceway was retarded by reduced feeding in order to provide fish of comparable size to match the hybrid. In 1973, 1974, and 1975, their mean weights at planting were, respectively, 10.8, 9.7, and 9.3 g (Table 2). In 1976 and 1977, normal hatchery feeding was resumed and the domestic strain weighed 16.8 and 25.2 g at planting.

Interstrain hybrids (NIP × DOM, DICK × DOM) were incubated and reared at Pembroke Hatchery. Growth of the NIP × DOM hybrid varied little from year to year and mean weight at planting ranged from 5.3 to 7.8 g. Growth of the DICK × DOM hybrid was more variable and fall fingerlings

TABLE 3. Recoveries by gillnetting and angling of planted brook trout from three study lakes (in the order domestic and Dickson × domestic hybrid). In Oram Lake, F_1 wild Nipigon strain were also planted.

	Year of planting					
	1973	1974	1975	1976	1977	Mean
	Little Minnow (92 m · ha^{-1} · yr^{-1})					
Mean weight (g) at planting		8.0	13.0	16.8	19.7	14.4
		11.1	14.2	10.1	6.8	10.6
Number planted per hectare		79	79	79	79	
		79	63	79	79	
Percent recovered		1.7	5.0	5.7	6.6	4.8
		12.3	18.2	3.7	11.0	11.3
Weight planted (kg)		5.6	9.1	11.8	13.8	
		7.8	8.0	7.1	4.8	
Weight caught/weight planted		0.3	0.8	0.4	0.5	0.5
		1.9	2.9	0.8	2.6	2.1
	Presto Lake (53 m · ha^{-1} · yr^{-1})[a]					
Mean weight (g) at planting	10.8	9.7	9.3	16.8	25.2	14.4
	5.8	7.3	6.1	10.1	4.2	6.7
Number planted per hectare	89	77	77	77	77	
	77	77	77	77	77	
Percent recovered	0.6	0.7	1.2	1.8	2.1	1.3
	1.8	1.8	2.0	0.8	1.8	1.6
Weight planted (kg)	15.0	11.6	11.2	20.2	30.2	
	7.0	8.8	6.1	12.1	5.0	
Weight caught/weight planted	0.1	0.2	0.3	0.5	0.1	0.2
	0.7	1.1	1.4	0.5	2.3	1.2
	Oram Lake (41 m · ha^{-1} · yr^{-1})					
Mean weight (g) at planting	10.8	9.7	10.6	10.1	19.7	12.2
(Dickson × Domestic)	5.8	7.3			5.7	6.3
(Nipigon)			6.2	8.6	5.5	6.8
Number planted per hectare	82	74	74	74	74	
	74	77			43	
			69	77	43	
Percent recovered	5.3	3.8	9.9	10.6	7.4	7.4
	11.5	6.5			7.9	8.6
			3.0	4.4	2.9	3.4
Weight planted (g)	24.1	19.4	21.2	20.2	39.4	
	11.6	15.3			6.5	
			11.6	17.9	6.4	
Weight caught/weight planted	2.5	0.8	2.0	2.0	0.7	1.6
	4.6	3.3			3.2	3.1
			1.3	0.8	1.3	1.1

[a]Gillnetting only.

ranged from 4.2 to 14.2 g at planting (Table 3).

In order to provide some wild strain progeny for testing, eyed eggs were incubated at the Maple Laboratory (where water temperatures permitted earlier hatching) and reared at the Harkness Laboratory, Lake Opeongo. The earlier start resulted in a larger fingerling for fall planting; F_1 wild Dickson strain reared at the laboratory averaged 5.7 g at planting compared with 3.3 g for those hatched and reared at Pembroke Hatchery (Table 4). DICK × NIP hybrids reared at the laboratory averaged 5.4 g at planting.

Brook trout were planted annually in September – early October during 1973–77. Prior to planting (3–30 d), the fish were anesthetized with ethyl *m*-aminobenzoate methanesulfonate (MS222) and finclipped. The adipose fin was excised from domestic brook trout; right or left ventral fins were removed from the hybrids on an alternate year basis. An exception was the DICK × NIP hybrid which received right or left pectoral clips. Samples of fish were dip-netted from the rearing trough and fork lengths were measured. Mean weight was determined by counting the number of fish in a 1-kg lot. Little Mykiss, Chipmunk, Rumley, and Presto lakes were planted by airdrop. Fish-carrying equipment and loading rates were as described by Fraser (1968). Fish planted in the other five lakes were transplanted by truck in oxygen-equipped tanks. The matched plantings were made at an overall rate of 150 fish/ha with several exceptions as noted (Tables 2, 3, 4).

Methods of Recovery

Six of the nine lakes were closed to angling and their fish populations were sampled annually with gill nets in June–July during 1974–80. Gillnetting effort within a lake was constant from year to year, but ranged from 92 $m \cdot ha^{-1} \cdot yr^{-1}$ in the smaller lakes to 41 $m \cdot ha^{-1} \cdot yr^{-1}$ in the larger lakes. The gill nets, of monofilament nylon, were 16 m long and 1.8 m deep. The net gang consisted of three 16-m sections of 51-, 64-, and 76-mm mesh (stretched measure).

Little Minnow, Oram, and Major lakes were fished by anglers who were contacted daily by a creel census clerk. These lakes were also sampled with the standard gill nets. All fish caught in the gill nets were brought to the laboratory for examination. Stomach contents of a subsample of the catch were preserved, and the stomach contents of the remainder were identified and recorded at the time of examination. Later, preserved stomach contents were identified; the organisms were separated into taxonomic groups, and the volume of each group was measured to the nearest 0.1 mL by

TABLE 4. Recoveries by gillnetting (Mykiss Lake) and gillnetting and angling (Major Lake) of matched plantings of domestic and F_1 wild Dickson strain brook trout. Wild Dickson × wild Nipigon hybrids were also planted in Mykiss Lake.

	Year of planting					
	1973	1974	1975	1976	1977	Mean
	Major Lake (46 $m \cdot ha^{-1} \cdot yr^{-1}$)[a]					
Mean weight (g) at planting						
Domestic	10.8	9.7	9.3	10.1	19.7	11.9
F_1 wild Dickson	3.6	3.2	2.4	4.9	2.5	3.3
Numbers planted per hectare	86	76	76	76	76	
	74	76	76	96	76	
Percent recovered	3.9	5.7	17.0	10.9	6.8	8.9
	5.2	7.6	18.1	12.4	8.8	10.4
Weight planted (kg)	24.5	19.4	18.6	20.2	39.4	
	7.0	4.4	4.8	12.4	5.0	
Weight caught/weight planted	0.4	0.6	1.3	0.9	0.3	0.7
	1.6	5.3	6.8	3.0	3.7	4.1
	Mykiss Lake (70 $m \cdot ha^{-1} \cdot yr^{-1}$)					
Mean weight (g) at planting						
Domestic	11.0	8.0	12.9	10.0	19.7	12.5
F_1 wild Dickson	3.6	6.0	6.4	9.7	2.9	5.7
Dickson × Nipigon	5.3	6.5	3.2	6.9	4.9	5.4
Number planted per hectare	82	51	51	102	51	
	72	51	51	51	44	
	11	51	51	57	62	
Percent recovered	3.1	4.0	4.1	4.1	4.8	4.0
	7.4	11.8	16.0	13.8	16.8	13.2
	6.2	8.0	13.8	6.7	14.7	9.9
Weight planted (kg)	21.2	9.6	15.5	24.0	23.6	
	6.1	7.2	7.7	11.6	3.0	
	1.4	7.8	3.8	9.3	7.2	
Weight caught/weight planted	0.8	1.1	0.6	1.2	0.5	0.8
	8.9	5.9	9.3	6.1	19.3	9.9
	7.0	4.7	20.1	5.2	8.4	9.1

[a]The gillnet gang fished in Major Lake included a 16-m section of 38-mm mesh to sample better the small (mean 3.3 g at planting) Dickson strain brook trout.

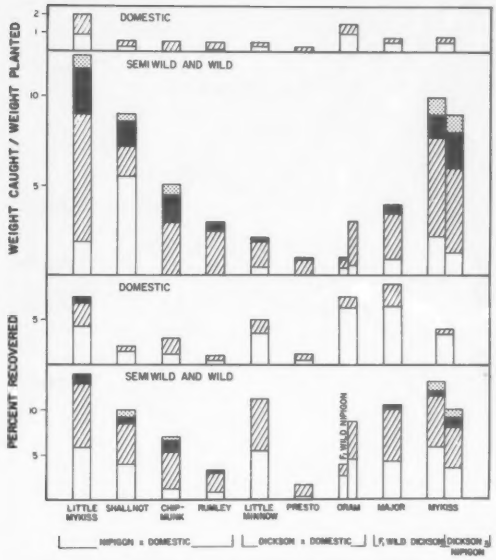

FIG. 1. Bottom panel: mean recoveries of five annual plantings of domestic and semiwild (or wild) strains of brook trout from nine study lakes. Top panel: ratio of weight recovered to weight planted. Clear areas in histograms, recoveries in year following planting ($n + 1$); hatched areas, in year $n + 2$; black areas, in year $n + 3$; and stippled areas, in year $n + 4$.

water displacement in a graduated cylinder. Volumes were pooled for each length group of fish and the composition of the contents was expressed as a percentage of the total volume of food measured. Percent frequency of occurrence of food items was based on stomachs examined at time of capture, combined with data on preserved stomach contents examined later.

The coefficient of condition (K) was computed: $K = W \times 10^5/L^3$, where W is the weight in grams and L is the fork length in millimetres.

Results

Recoveries — Domestic Strain versus NIP × DOM Hybrid

The mean recovery of NIP × DOM hybrids was two to four times greater than that of the domestic strain in the four lakes in which they were stocked (Table 2). The hybrid also survived longer, some individuals for 4–5 yr after planting, whereas few domestic strains survived more than 2 yr (Fig. 1). The greater survival and longevity of the hybrid resulted in weight returns 6–15 times greater than that of the domestic brook trout (Table 2). The highest yield was from Little Mykiss Lake where 12.3 kg of hybrid strain was recovered for each kilogram planted, compared with 2.1 kg per kilogram of domestic strain planted. Similar differences occurred in the other three study lakes in which the return of domestic strain was only 0.4–0.6 kg per kilogram planted, compared with 3.1–9.1 kg per kilogram of NIP × DOM hybrid planted (Table 2).

Recovery of the annual plantings varied considerably in the lakes that contained few competitive species. For example, recovery of the domestic strain in Little Mykiss Lake ranged from 2.3 to 18.3% and the NIP × DOM hybrid from 3.1 to 25.0% (Table 2). In contrast, recoveries in Chipmunk and Rumley lakes, which contained competitive species, were low and varied little from year to year.

Domestic Strain versus DICK × DOM Hybrid

The above strains were tested in three lakes with variable results. In Little Minnow Lake, where planted trout faced competition with an abundant yellow perch population, a mean recovery of 4.8% of the domestic strain and 11.5% of the hybrid was taken by gill nets and angling. Angling accounted for 70% of the domestic strain and 62% of the hybrids recovered. Most of the domestic recovery was made within a year of planting, whereas the hybrid recovery was taken over a period of 2 yr following planting (Fig. 1). In terms of weight, only 0.5 kg of domestic strain was recovered for each kilogram planted; the hybrid returned 2.1 kg per kilogram planted.

Both domestic strain and hybrid performed poorly in Presto Lake and mean recoveries of five annual plantings were 1.3 and 1.6%, respectively. Presto Lake is an exceptionally deep lake (35.7 m) and its precipitous shoreline apparently offered little habitat for either strain, or, for that matter, native species.

Three brook trout strains were tested in Oram Lake (Table 3): domestic (five plantings), DICK × DOM hybrid (three plantings), and F_1 wild Nipigon (three plantings). Approximately 8% of both the domestic strain and the hybrid were recovered, compared with a 3.4% mean recovery of the F_1 wild Nipigon strain. Most of the domestic brook trout were caught within a year of planting, 47% of the recovery by angling, whereas more of the hybrids were taken 2 yr after planting, 78% of the recovery by angling.

Domestic Strain versus F_1 Wild Dickson (and DICK × NIP Hybrid)

Matched plantings of F_1 wild Dickson strain and domestic strain were assessed by gillnetting and angling in Major Lake. Although the domestic strains were much larger at planting (11.9 g compared with 3.3 g for Dickson), the mean recoveries over the 5 yr of plantings were similar, 8.9 and 10.4%, respectively (Table 4). Much of the domestic strain recovery was made in the year following planting, 72% by gill nets and 28% by angling. The recovery of wild Dickson strain was spread over 3 yr, 40% in year $n + 1$, 57% in $n + 2$, and 3% in $n + 3$. Seventy-nine percent of the Dickson strain recovery was taken by angling. In terms of weight, F_1 wild Dickson returned 4.1 kg per kilogram planted, compared with 0.7 kg per kilogram of domestic strain planted.

Three brook trout strains were planted annually in Mykiss Lake during 1973–77. F_1 wild Dickson strain (mean weight 5.7 g) and Dickson × Nipigon hybrids (5.4 g), which were reared at the Harkness Laboratory, were planted together with domestic strain (12.5 g) reared at Pembroke Hatchery. The

TABLE 5. Mean fork length (cm) at age 2 of various strains of brook trout planted in nine study lakes during 1973–77. Standard errors (in parentheses) are based on five or more fish.

Year of planting	Shallnot		Little Mykiss		Chipmunk		Rumley		Little Minnow		Presto		Oram			Major		Mykiss	
	DOM	NIP × DOM	DOM	NIP × DOM	DOM	NIP × DOM	DOM	NIP × DOM	DOM	DICK × DOM	DOM	DICK × DOM	DOM	DICK × DOM	Wild Nipigon	DOM	Wild Dickson	DOM	Wild Dickson	DICK × NIP
1973	38.2		38.0	42.0	31.0	29.0	36.1	35.5			26.1	25.3	31.9	31.5		26.6	22.4	33.3	31.5	34.6
			(0.59)	(0.57)	(0.76)	(0.37)		(0.28)			(1.00)	(0.66)	(0.84)	(1.05)		(1.13)	(0.75)	(0.72)	(0.23)	(0.70)
1974	35.3	40.7	38.6	39.0	28.4	26.9	34.2	34.1		27.6	26.2	31.5	34.6	37.6		25.5	22.9	32.2	34.8	35.9
	(0.52)	(0.36)		(0.66)	(0.79)	(0.25)	(0.34)	(0.47)		(0.36)	(0.78)	(0.63)		(0.78)		(1.00)	(0.73)		(0.48)	(0.71)
1975	42.1	40.3	33.1	36.7	29.1		32.9	35.3	26.9	28.0	27.3	29.9	35.4		32.7	24.5	24.0	34.2	34.5	33.2
		(0.32)	(0.68)	(0.41)	(0.28)		(0.53)	(0.46)	(0.42)	(0.32)	(0.56)	(0.56)	(0.59)		(1.06)	(1.00)	(0.60)		(0.43)	(0.28)
1976	36.6	36.2	33.7	35.1	30.9	30.6	36.4	37.9	25.4	25.7	32.6	34.2	35.1		29.9	25.2	24.0	34.5	37.8	36.2
		(0.31)	(0.29)	(0.21)	(0.36)	(0.27)		(0.35)	(0.67)	(0.38)	(0.88)	(1.41)	(0.71)		(0.52)	(0.94)	(0.61)	(0.98)	(0.44)	(0.41)
1977	37.6	35.7	33.4	33.7	33.2	31.9		37.5		27.8	29.5	33.3	29.1	33.1	30.9		24.1	30.0	30.3	32.6
		(0.49)	(0.83)	(0.26)	(0.69)	(0.25)		(0.45)		(0.50)		(0.69)		(1.21)	(0.89)		(0.55)		(0.37)	(0.21)
Mean	38.0	38.2	35.4	37.3	30.5	30.9	34.9	36.1	26.2	27.3	28.3	30.8	33.2	34.1	31.2	25.5	23.5	32.8	33.8	34.5

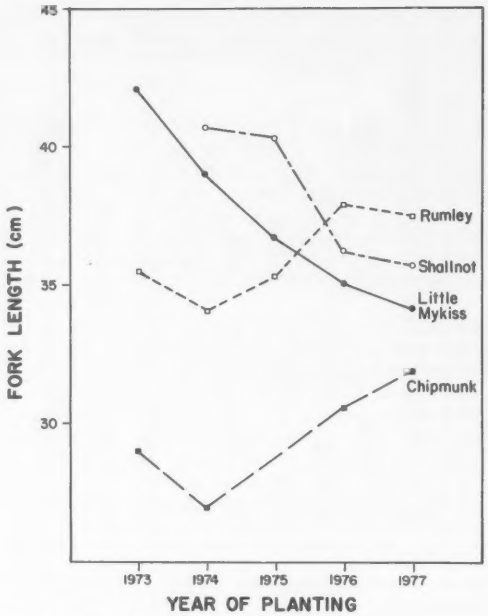

FIG. 2. Mean fork lengths at age 2 of annual plantings (1973–77) of NIP × DOM hybrids in four study lakes.

recovery of the wild strain and the hybrids by gillnetting was two to three times greater than the domestic strain recovery and, being spread over a period of 4 yr (Fig. 1), resulted in a weight return of 9–10 kg for each kilogram planted, compared with about 1 kg per kilogram of domestic strain planted (Table 4). The recovery of F_1 wild Dickson was slightly higher than the recovery of the Dickson × Nipigon hybrids.

GROWTH

Domestic strain and NIP × DOM hybrids planted in the same lake grew at similar rates. Both strains were fully vulnerable to gill nets and angling at age 2, and mean lengths of fish caught at this age are presented in Table 5. Although there was considerable variation in growth of the different years' plantings, the matched plantings followed similar trends (i.e. a planting of NIP × DOM hybrid that grew rapidly was usually accompanied by rapid growth of the matched domestic strain).

Lengths attained by the various NIP × DOM hybrids at age 2 demonstrate the variability in growth of different years' plantings (Fig. 2). In Shallnot and Little Mykiss lakes, growth rate of the NIP × DOM hybrid decreased steadily from the 1973 to 1977 planting. These lakes contain no competitive species, and it is likely that the reduced growth of the latter plantings was associated with their higher survival rate or due to competition from survivors of the earlier plantings. This situation did not hold for Rumley and Chipmunk lakes, where trout survival was apparently limited by native competitive species. Growth rate of the NIP × DOM hybrid was rapid in

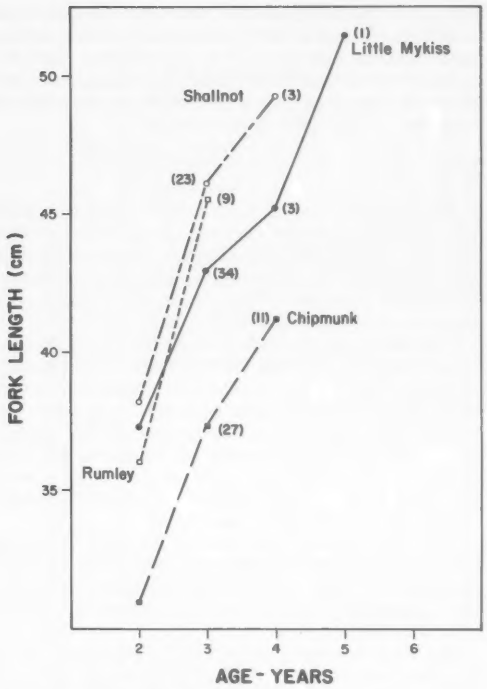

FIG. 3. Mean fork length at various ages of NIP × DOM hybrids planted in four study lakes. Age 2 values are based on 100+ fish; older fish samples are in parentheses.

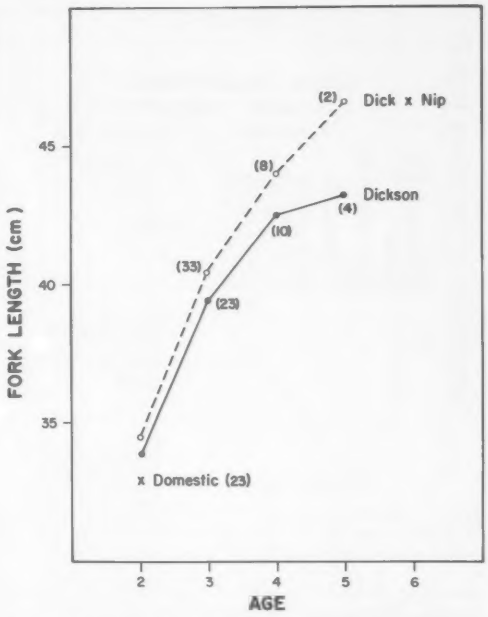

FIG. 4. Mean fork length at various ages of domestic, F_1 wild Dickson, and DICK × NIP hybrids planted in Mykiss Lake. Age 2 values are based on 100+ fish; older fish samples are in parentheses.

Shallnot, Little Mykiss, and Rumley lakes and slow in Chipmunk Lake. The slow growth in Chipmunk Lake was most likely due to competition from a white sucker population. Hybrid trout planted in Rumley Lake survived poorly in the face of competition with yellow perch and pumpkinseed, but the survivors apparently learned to utilize young-of-the-year yellow perch and pumpkinseed for food and grew rapidly. A few of the NIP × DOM hybrids survived to reach ages 4–5 and lengths over 45 cm (Fig. 3).

In Little Minnow, Presto, and Oram lakes, in which domestic strain and DICK × DOM were matched, only minor differences in rate of growth between the stocks are evident (Table 5). Few fish of either strain survived beyond age 2. Growth was slow in Little Minnow Lake where planted trout competed with yellow perch.

First-generation wild Dickson strain were matched with domestic strain in Major and Mykiss lakes. Both strains grew slowly in Major Lake and rapidly in Mykiss Lake (Table 5). Slow growth in Major Lake was likely due to competition with white suckers. Competition was not a factor in Mykiss Lake and both strains, together with the DICK × DOM hybrid, grew rapidly. However, few domestic strain survived beyond age 2 whereas some wild Dickson and DICK × NIP hybrids survived to age 5 in Mykiss Lake (Fig. 4).

There is evidence that growth in the hatchery can be a determinant of growth after release in the lake. The F_1 wild Dickson strain planted in Mykiss Lake ranged from 2.9 to 9.7 g in weight at time of planting during 1973–77. When the length, at age 2, of the survivors of these plantings was plotted against their size at planting an excellent correlation resulted (Fig. 5). A less significant correlation is also evident for the DICK × NIP hybrid planted in Mykiss Lake during the same period. Similar correlations cannot be demonstrated for the other hybrids because their size at planting varied little. Size of the domestic strain at planting varied from year to year, but it was not related to size at recapture.

COEFFICIENT OF CONDITION

Coefficients of condition computed for the various strains of brook trout collected at age 2 are summarized in Table 6. Domestic strain exhibited a slightly higher coefficient than the hybrids in the majority of comparisons. In Mykiss Lake, however, there was little difference between the domestic and wild strains.

Coefficient of condition differed among the lakes, with highest values recorded for trout planted in lakes containing only minnows, and lower values for trout in lakes containing more competitive species. An exception was Rumley Lake where, in spite of competition with yellow perch, planted brook trout were in good condition.

The hybrids NIP × DOM and DICK × DOM, although not planted in the same lake, possessed similar condition factors when planted in similar types of lakes. The lowest condition factor was noted in the F_1 wild Dickson strain

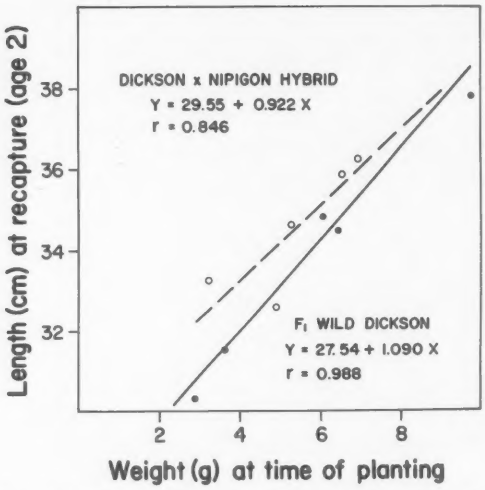

FIG. 5. Relationship between weight at time of planting and length at recapture (age 2) of F_1 wild Dickson strain and DICK × NIP hybrids planted annually in Mykiss Lake during 1973–77.

planted in Major Lake, where it faced competition from a sizeable white sucker population (Table 6). However, the same wild strain attained a moderately high condition factor when planted in Mykiss Lake, where competition was much less.

Condition factors fluctuated from one year's planting to the next in the same lake. Generally, there was no definite trend in difference except in Little Mykiss Lake, where condition factor decreased from the 1973 to 1977 plantings (Table 6). A concurrent decrease in average length also occurred. Overall, the data suggest an apparent correlation between condition factor and growth.

FOOD

In seven lakes, few differences in food habits were noted between strains planted in the same lake; trout that survived essentially ate the same food. Therefore, stomach analyses of wild and domestic trout were combined in summary, and are illustrated in Fig. 6 and 7. These figures show, however, that trout diet differed considerably from lake to lake.

Dominant foods, depending on the lake, were plankton (largely *Daphnia* sp.), fish, Diptera (mainly Chironomidae), Trichoptera, and leeches. Usually, 80% of the volume of food eaten consisted of three (sometimes two) of the above taxonomic groups. In lakes containing only minnow species, brook trout ate a greater variety of organisms than trout planted in lakes containing yellow perch and white suckers. Food items of lesser importance included Odonata, Ephemeroptera, Coleoptera, and crayfish.

There was little difference between the diet of small and large brook trout in the same lake (Fig. 6 and 7). Their dominant food items were similar but sometimes differed in order of importance in the diet. Only the larger brook trout utilized crayfish, however.

Fish were an important component of brook trout diet in five lakes. In Oram Lake, all three strains preyed heavily on minnows, chiefly northern redbelly dace (*Phoxinus eos*). This

TABLE 6. Average coefficient of condition (K) at age 2 of various strains of brook trout in nine study lakes. Averages are based on samples of at least five fish. Values in parentheses are averages of the domestic strain.

	Year of planting					
	1973	1974	1975	1976	1977	Mean
			NIP × DOM Hybrid			
Little Mykiss	1.46	1.49	1.31	1.29	1.21	1.35
	(1.58)		(1.35)	(1.33)	(1.40)	(1.42)
Shallnot		1.50	1.42	1.42	1.43	1.44
		(1.55)				
Chipmunk	1.25	1.13	1.14	1.14	1.28	1.19
	(1.20)	(1.17)	(1.29)	(1.20)	(1.29)	(1.23)
Rumley	1.25	1.28	1.47	1.30	1.40	1.34
		(1.33)	(1.43)			(1.38)
			DICK × DOM Hybrid			
Little Minnow	1.21	1.31	1.24	1.22		1.25
	(1.21)					
Presto	1.17	1.32	1.40	1.40	1.48	1.35
	(1.11)	(1.33)	(1.34)	(1.43)		(1.30)
Oram	1.54	1.47	1.54		1.38	1.48
	(1.59)		(1.55)	(1.36)		(1.50)
			F_1 Wild Dickson			
Major		1.07	1.03	1.03	1.07	1.05
		(1.09)				
Mykiss	1.25	1.32	1.34	1.33	1.17	1.28
	(1.30)	(1.27)		(1.32)	(1.20)	(1.27)
DICK × NIP	1.27	1.30	1.21	1.26	1.11	1.23

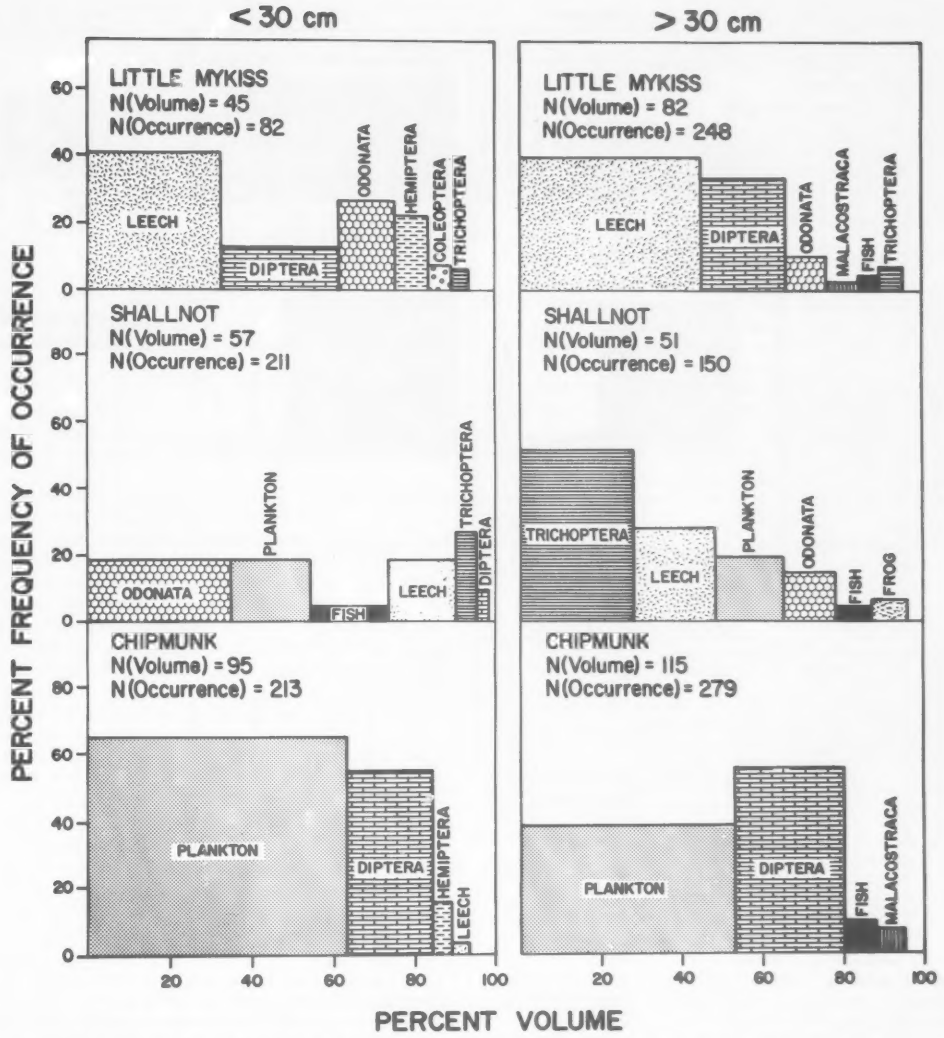

FIG. 6. The food of small (<30 cm) and large (>30 cm) brook trout caught in three study lakes during June and July, 1974–79. N = number of fish examined and includes NIP × DOM hybrids and domestic strain.

species is abundant in other study lakes but is little utilized during the summer, except in Little Minnow Lake. Its availability to planted brook trout in Oram Lake possibly accounts for the relatively high 7.4% recovery of the domestic strain from this lake. Brook trout in Rumley and Presto lakes ate yellow perch and pumpkinseed, mostly young-of-the-year fish. An example of the heavy predation that may occur is found in the July, 1979, gillnet sample from Presto Lake. Fifteen brook trout (30–40 cm) were found to contain a total of 310 g of fish, almost entirely young-of-the-year yellow perch. The content of individual stomachs ranged from 4.5 to 41.0 g in weight.

Diet differed between domestic strain and hybrids in only two lakes. In both lakes, the hybrid trout preferred fish, yellow perch and pumpkinseed in Rumley Lake and redbellied dace (mainly) in Little Minnow Lake; the domestic strain were dependent on Trichoptera (Fig. 8).

Although our data provide an account of food habits for June–July only, they strongly indicate that with two exceptions, food habits of the matched brook trout strains are sim-

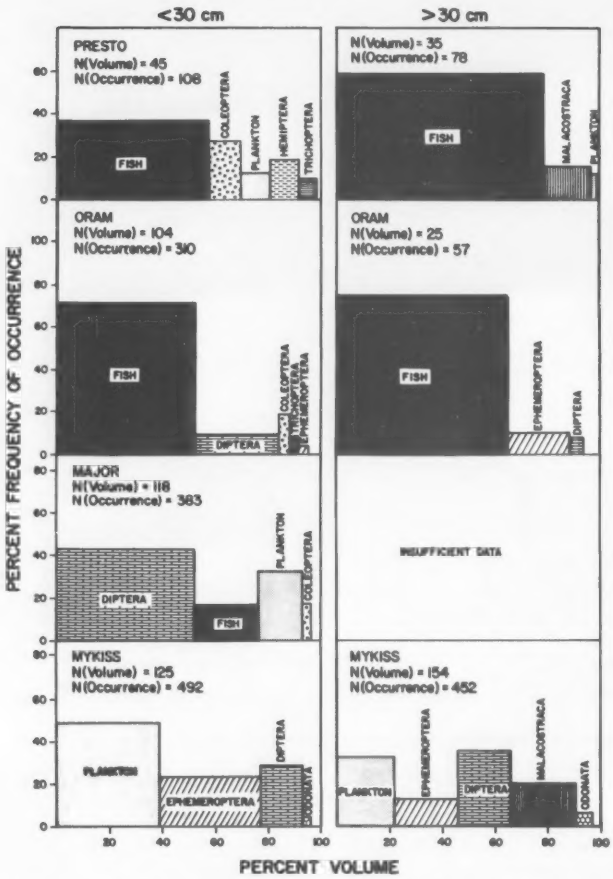

FIG. 7. The food of small (>30 cm) and large (>30 cm) brook trout caught in four study lakes during June and July, 1974–79. N = number of fish examined and includes hybrid (or wild) and domestic brook trout.

ilar within a lake. Also, small and large brook trout are dependent on the same several organisms within a lake. However, diets differ considerably from lake to lake.

Discussion

The results of this study confirm a conclusion of earlier studies (Fraser 1972, 1980) that the domestic brook trout strain routinely planted in Ontario waters survives poorly after release. In six study lakes, hybrids (and wild strains) were recovered at rates two to four times greater than the domestic strain. In three other lakes, they were caught at about the same rate. Hybrids and wild strain lived longer than the domestic strain. Most domestic trout were caught in the year following planting, whereas recoveries of hybrids and wild strain were spread over 3–4 yr. The greater recovery rates and longevity of the hybrids and wild strain resulted in weight returns much higher than those of the domestic strain.

Both domestic strain and hybrids (and wild strain) fared best where competition from resident fishes was least. Lakes containing only minnows and sticklebacks yielded high returns of brook trout in numbers and weight, whereas lakes containing competitive species (yellow perch, white sucker) yielded low returns.

Although there was considerable fluctuation in the percentage recovery of the various strains from year to year, there was a definite general tendency for the 1973 and 1974 plantings to result in the lowest recoveries and the 1975 plantings to have the highest recoveries with the 1976 and 1977 plantings being somewhat intermediate. A possible cause of this trend could be predation on the earlier plantings by splake (ages 3–5) which were fish carried over from earlier studies (Fraser 1980) in six of the study lakes. Few of these potential predators were extant at fall planting in 1975 and thereafter.

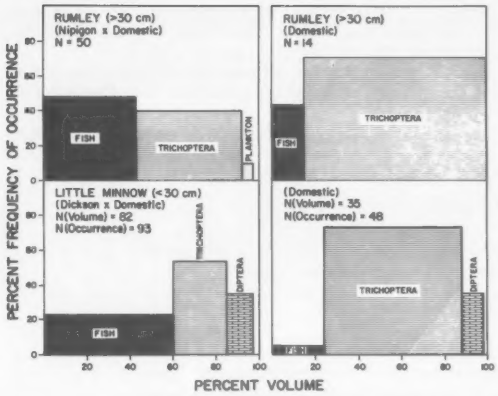

FIG. 8. The food of (a) hybrid and (b) domestic strain brook trout caught in Rumley and Little Minnow lakes during June–July, 1974–79. N = number of fish examined.

It should be noted, however, that there was no direct evidence of predation by splake on planted brook trout.

Size of trout at planting, within the size ranges used, had no apparent relationship to subsequent recovery. In nearly all comparisons, the domestic strain was larger at time of planting than the matched hybrid or wild strain. Mean weight of the domestic plantings ranged from 9.3 to 25.2 g, but there were no corresponding differences in percentage recovered. Neither were there differences in the recovery of the hybrids or wild strain which could be attributed to size of the fish at planting. Flick and Webster (1976) also noted that size did not play an overriding role in shaping survival in their studies.

Although size at planting had little relationship to survival, it apparently influenced growth of the planted trout in the lake. This was demonstrated in Fig. 5 for both the DICK × NIP hybrid and the wild Dickson strain planted in Mykiss Lake. The lots of fish that had grown rapidly in the hatchery maintained their size advantage in the lake.

Both domestic strain and the matched hybrid grew at the same rate within a lake, but there were considerable differences in growth rate among the lakes. Rapid trout growth occurred in lakes containing minnows and sticklebacks; slowest growth was noted in lakes containing white suckers.

It appears that even short-term domestication may reduce a wild strain's ability to survive in the wild. The "domestic" strain used in our comparisons became 25% wild Nipigon strain about 15 yr ago. Yet, when it was matched with a Nipigon × domestic hybrid (50% Nipigon), its recovery was only 25–50% that of the hybrid. Smith (1957), on the basis of studies on planted rainbow trout (*Salmo gairdneri*), cautioned that even short-term exposure of wild trout to hatchery practices could lead to a change in its behavior. More recently, Reisenbichler and McIntyre (1977) reported genetic differences in growth rate and survival between offspring of hatchery and wild steelhead trout. The hatchery fish were not more than two generations removed from wild stocks. After studying genetic changes in hatchery stocks of brown trout (*Salmo trutta*), Ryman and Stahl (1980) emphasize the importance of using large numbers of actual, as well as effective, parents to avoid inadvertent genetic changes and inbreeding.

The performances of the three hybrids and the F_1 wild Dickson strain were superior to that of the domestic brook trout in this study. The top performer, however, was the NIP × DOM hybrid by virtue of more extensive testing than the other hybrids. The DICK × DOM hybrid showed potential and is receiving additional testing. Although the DICK × NIP hybrid and the F_1 wild Dickson strain also showed potential, problems of hatchery rearing and inadequate supply of brood stock could curtail their use.

Hybridization appears to be the path to follow to achieve greater salmonid production from the Ontario lakes routinely planted with domestic strain brook trout. Natural reproduction is not a factor in the majority of these lakes, as they lack suitable spawning areas for brook trout. Therefore, in using hybrids, genetic variability is exploited, without harm to native brook trout, to increase heterosis and production. The performance of the interstrain NIP × DOM hybrid in this study, and, as well, the performance of the interspecies hybrid F_1 splake in an earlier study (Fraser 1980), qualify them for consideration as replacements for the domestic brook trout strain currently in use. The studies of Flick and Webster (1976) in Adirondack Mountain lakes provide supportive evidence in favor of wild and/or hybrid stocking over use of inbred domestic strains of brook trout.

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Survival, Growth, Spawning Distribution, and Movements of Introduced and Native Lake Trout (*Salvelinus namaycush*) in Two Inland Ontario Lakes[1,2]

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This paper attempts to develop a biological basis for the management of stocks of lake trout (*Salvelinus namaycush*). Recent studies of the influence of genetic differences on the survival of planted stocks of trout and of the spatial distribution and movements of lake trout populations are reported. The genetic origin of planted lake trout influenced their survival in four Ontario lakes, whereas water hardness of the rearing hatchery had little effect. Survival also appeared to be influenced by the status of the native population but growth rates of native and introduced trout were similar. Age of first maturity appeared to differ between stocks in Lake Simcoe. Studies with both numbered and sonic tags in Lake Opeongo suggested that lake trout do not home to their natal shoal. Differences in total distances travelled were observed between sexes, but both males and females moved between shoals at spawning time. In Lake Simcoe, planted trout dispersed widely, colonizing spawning shoals up to 30 km from release sites, and no differences between stocks in time of spawning could be detected despite apparent differences in the home lakes. Temperature influenced spawning time and accounted for most of the timing variation between two allopatric lake trout stocks.

Key words: lake trout, native, introduced, survival, growth rate, spawning distribution, movement, homing

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On trouvera dans l'article qui suit le compte rendu des efforts en vue de trouver une base biologique à la gestion des stocks de touladis (*Salvelinus namaycush*). Nous signalons les études récentes sur l'influence des différences génétiques sur la survie des stocks de touladis ensemencés ainsi que les études sur la distribution spatiale et les déplacements des populations de cette espèce. L'origine génétique des touladis introduits a influencé leur survie dans quatre lacs de l'Ontario, tandis que la dureté de l'eau de l'établissement de pisciculture eut peu d'effet. La survie semble également influencée par l'état de la population indigène, mais les taux de croissance des touladis indigènes sont semblables à ceux des sujets introduits. L'âge de première maturité semble différer d'un stock à l'autre dans le lac Simcoe. Des études menées avec des étiquettes tant numérotés qu'ultrasoniques dans le lac Opeongo suggèrent que le touladi ne revient pas vers les hauts-fonds natals. Nous avons observé des différences entre sexes dans les distances parcourues, mais les mâles et les femelles se déplacent d'un haut-fond à l'autre au moment de la ponte. Dans le lac Simcoe, les touladis ensemencés se dispersent sur une grande étendue, colonisant des hauts-fonds de ponte jusqu'à 30 km des points de mise en liberté. En dépit d'apparentes différences dans les lacs d'origine, nous n'avons pu détecter de différences entre stocks quant au temps de la ponte. La température

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influence ce temps et rend compte de la majeure partie de la variation entre deux stocks allopatriques de touladis.

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MARTIN and Olver (1976, 1980) discuss the need for management and rehabilitation of lake trout (*Salvelinus namaycush*) communities, which are threatened by eutrophication, exploitation, introduction of exotics, and acidification. Loftus (1976) argues that recognition of the genetic differences between lake trout stocks is critical to the development of these initiatives. Larkin (1972) defines a stock as "a population of organisms which, sharing a common environment and participating in a common gene pool, is sufficiently discrete to warrant consideration as a self-perpetuating system which can be managed." In the present paper, we discuss several recent studies which contribute to a biological basis for a stock concept for the management of lake trout communities.

Until fairly recently, managers have ignored the implications of genetic differences between allopatric and sympatric populations of lake trout. Haskell et al. (1952) showed that adaptive differences between allopatric stocks of lake trout influence their survival and growth when they are planted. The SCOL Symposium (Loftus and Regier 1972) focused attention on the "fishing-up" process as one cost of ignoring the existence of discrete sympatric stocks in the Great Lakes (Behnke 1972; Lawrie and Rahrer 1972; Regier and Loftus 1972). Loftus (1976) suggests that lack of appropriate brood stocks for lake trout could delay rehabilitation in the Great Lakes. Cultured lake trout have been extensively planted to rehabilitate stressed populations, but the results have been extremely variable, and the nature of the differences between stocks that determine relative fitness in a particular environment is not known. We will present evidence from two studies that genetic differences between cultured lake trout stocks influence their survival, and we will argue that the adaptive differences between stocks that influence survival and reproduction are ecologically coarse-grained rather than fine-grained (MacArthur and Wilson 1967).

An understanding of the breeding structure of lake trout populations is central to the development of a stock concept. Olver and Lewis (1977) found few reports of successful reproduction by planted lake trout. Several studies have suggested the hypothesis that lake trout home to spawning shoals and planted lake trout are unable to locate suitable spawning areas (Brown et al. 1981; Horrall 1981). The observed differences between stocks in time of spawning also suggest that planted lake trout may not spawn at an appropriate time for survival of the progeny. We will discuss results from two studies that examine these hypotheses and lead to a new conception of the breeding structure of lake trout populations.

Comparison of Survival of Planted Stocks

LAKE OPEONGO PLANTINGS

An experiment was initiated in Lake Opeongo during 1970 with three objectives: (1) to test the hypothesis that the genetic origin of planted lake trout stocks influences survival and recruitment to angling fisheries; (2) to evaluate the use of 2-yr-old lake trout for planting; few of the yearlings planted prior to 1970 survived, despite attempts to vary the time, location, and method of planting (Martin and Fry 1972, 1973); (3) to test the hypothesis that differences in survival of planted stocks are related to adaptations, during culture, to water chemistry, particularly water hardness (Phillips 1959).

Lake trout eggs were collected and fertilized during the fall of 1970 and 1971 from Lake Opeongo (45°42′N, 78°22′W) and Lake Simcoe (43°60′N, 79°45′W). Lake Opeongo (Fig. 1) is a softwater lake on bedrock of the Madawaska Highlands; total dissolved solids (35 mg/L) and alkalinity (4 mg $CaCO_3$/L) are low and the water is slightly acidic (average pH 6.6) (Martin and Fry 1972, 1973). Lake Simcoe (Fig. 2) is a hardwater lake on the limestone and shale of the St. Lawrence Lowlands; total dissolved solids (200 mg/L) and alkalinity (125 mg $CaCO_3$/L) are relatively high and the water is alkaline (pH 8.3).

Each stock was reared for ~ 24 mo after hatching in two different environments: (1) a softwater hatchery (Pembroke Fish Culture Station, hardness 41); (2) a hardwater hatchery (Wiarton and Chatsworth Fish Culture Stations, hardness 260 and 230, respectively). Eggs were hatched and the fry reared for ~ 6 mo at Wiarton before being transferred to Chatsworth.

The 2-yr-old lake trout were planted in three Algonquin Park lakes (Table 1). Each lot was distinctively finclipped, and the 1973 and 1974 plantings were to be differentiated by the age at capture. Opeongo–Chatsworth and Simcoe–Chatsworth fish were planted during 1974 in Brewer and Costello lakes (Fig. 1), which are small (0.41 and 0.34 km^2, respectively) lakes chemically similar to Lake Opeongo (Scheider 1978). Planted trout were recovered either by anglers, who were interviewed as part of the intensive creel census on Lake Opeongo (Martin and Fry 1972), or with gill nets during routine monitoring of fish communities.

A total of 92 planted lake trout were recovered from Lake Opeongo between 1973 and 1979, and 8 newly planted fish were recovered from the stomachs of larger trout during May and June of 1973, for a total recovery of 0.5% of the planted trout (Table 2). The use of 2-yr-olds, versus yearlings, does not appear to have substantially increased the survival and recruitment of planted lake trout.

The genetic origin and rearing environment of only 69 of the recovered lake trout could be determined, because of fin regeneration (Table 3). However, the results suggest that a greater proportion of the Opeongo stock were recovered, and similar differences were observed in both Brewer and Costello lakes (Table 4). These results support the hypothesis that genetic differences between lake trout stocks influence their survival. Relative proportions of the two stocks did not change between 1973–76 and 1977–79 ($\chi^2 = 0.04$, $P = 0.95$), which indicates that the differential mortality may occur in the first few years after planting (Table 5).

The similarity in the returns of planted lake trout from the two hatcheries suggests that the rearing environment had little influence on survival relative to the effects of genetic differ-

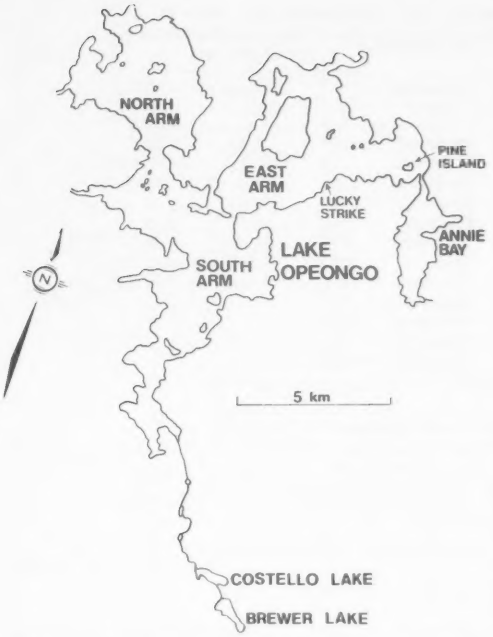

FIG. 1. Opeongo, Brewer, and Costello lakes in Algonquin Park, Ontario.

ences between stocks (Table 3).

The ages and lengths of 72 planted lake trout were compared with those of native lake trout, which were caught by anglers during 1979 (Fig. 2). Growth of planted and native fish was similar, and differences between stocks and between hatcheries in growth rate were not obvious, although the numbers of recovered fish in each case were small.

LAKE SIMCOE PLANTINGS

Lake trout eggs were collected annually from Lake Simcoe during the 1950s and 60s for general distribution in Ontario. By 1970, lack of mature lake trout at traditional spawning shoals rendered the operation ineffective. Origins of hatchery trout released prior to 1950 (MacCrimmon and Skobe 1970) are uncertain, and since 1974, lake trout from three different parental origins have been introduced: (1) Clearwater Lake, Manitoba (54°05′N, 101°00′W); (2) Hills Lake Fish Culture Station near Englehart, Ontario; and (3) Lake Manitou, Ontario (45°70′N, 82°00′W). The Clearwater and Manitou fish were reared from wild eggs at Chatsworth Fish Culture Station. The Hills Lake strain is third generation domestic, descendent from Lake Superior stock, although the exact source is unknown. They are referred to as being of Lake Superior origin in the following text and tables. The plantings of Superior strain trout were from eggs collected from 6- and 7-yr-old hatchery stock.

Lake Simcoe (Fig. 3) has an area of 725 km^2, mean and maximum depths of 17 and 40 m, respectively, and extensive

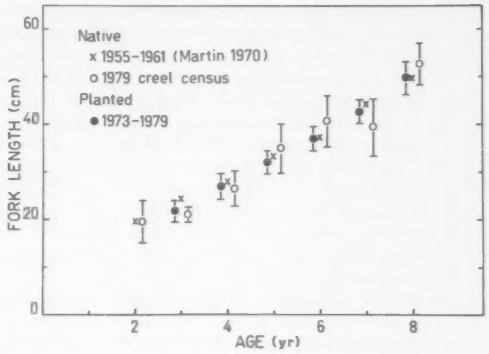

FIG. 2. Fork lengths of planted and wild native lake trout in Lake Opeongo. Means ± 1 SD and sampling dates are indicated.

shoreline shoals of limestone boulders. The lake is mesotrophic and supports a diverse fish community (MacCrimmon and Skobe 1970).

Survival of planted lake trout — Stocking information for several introduced lake trout stocks and their relative contribution to the winter angling fishery are given in Table 6. Assuming the annual winter harvest of hatchery lake trout to be about 4000 fish during this study period (DesJardine and Lawrence 1979), approximate returns can be calculated for each planting. For example, twenty-five 4-yr-old Manitoba strain fish were present in a sample of 48 angled lake trout in 1977; therefore, the total number caught equals 2083 (25/48 × 4000) and the rate of return is 4.2%. Rate of return from the winter fishery is highest at age 4, averaging 3.1% for the plantings shown. The majority of captures are from ages 4−7 inclusive, although ages 3−8 are represented in the catch.

Of the groups represented in Table 6, the largest contributions to the winter angling fishery and the highest percent returns have been made by Manitoba and Simcoe stocks. Each of the four parental stocks has contributed to the winter fishery. Superior stock has contributed least strongly, indicating higher mortality relative to the others. Assuming fixed vulnerability to angling, returns of Manitoba stock (ages 4−7) reflect a total mortality rate of 0.50 yr^{-1}.

Contribution of the various planted stocks to the lake trout spawning population from 1976 to 1980 is summarized in Table 7. Catch per unit effort (CUE) (adjusted to a common stocking rate) is generally highest at ages 5+ and 6+. Highest rates of recapture have been for Simcoe and Manitoba stocks at 2 fish per net night. In three separate plantings, Simcoe stock contributed most strongly at age 6+ independent of age at release (i.e. 1 versus 2 yr old), whereas Manitoba stock was most abundant at age 5+. Both stocks first appeared at shoal areas in large numbers at age 5+ with males forming 60% of the spawning runs, suggesting this to be the age of first maturity. At 6+, females dominated the runs of both stocks, indicating a similar pattern of maturity, but a greater proportion of the total Manitoba stock appears to have matured at age 5+.

Lake Simcoe stock released as yearlings and 2-yr-olds were

TABLE 1. Summary of records of lake trout planted in three Algonquin Park lakes, 1973–74.

Lake	Date	Stock	Fish culture station	Planted lake trout No.	Average length (cm)	SD
Opeongo	May 1–3, 1973	Opeongo	Pembroke	2500	16.02	1.62
			Chatsworth	0		
		Simcoe	Pembroke	2500	16.44	1.90
			Chatsworth	2725	18.14	2.38
	May 13–15, 1974	Opeongo	Pembroke	2500	16.13	2.45
			Chatsworth	2436	19.59	3.39
		Simcoe	Pembroke	2500	17.52	1.80
			Chatsworth	2458	18.49	1.78
Costello	May 28, 1974	Opeongo	Chatsworth	851		
		Simcoe	Chatsworth	1424		
Brewer	May 28, 1974	Opeongo	Chatsworth	851		
		Simcoe	Chatsworth	1424		

TABLE 2. Summary of returns of planted lake trout in Algonquin Park lakes, 1973–79.

Lake	Year	Opeongo stock		Simcoe stock		Unknown stock	Total recoveries
		Pembroke[a]	Chatsworth[b]	Pembroke	Chatsworth		
Opeongo	1973	0	0	2	0	1	3
	1974	4	2	0	2	0	8
	1975	2	0	0	1	5	8
	1976	9	6	2	0	8	25
	1977	10	5	3	1	5	24
	1978	4	3	2	0	0	9
	1979	7	0	3	1	4	15
Brewer	1975	—	14	—	7	1	22
	1976	—	4	—	0	0	4
	1977	—	1	—	0	0	1
Costello	1975	—	2	—	4	0	6
	1976	—	4	—	1	0	5
	1977	—	8	—	4	0	12
	1978	—	1	—	1	0	2

[a]Reared at Pembroke Fish Culture Station.
[b]Reared at Wiarton/Chatsworth Fish Culture Station.

TABLE 3. Recaptures of lake trout of different parental origin and rearing histories from Lake Opeongo, 1973–79.

Lake of stock origin	Rearing history		Totals
	Pembroke no. (%)[a]	Chatsworth no. (%)	
Opeongo	36 (0.7)	16 (0.7)	52 (0.7%)
Simcoe	12 (0.2)	5 (0.1)	17 (0.2%)
Totals	48 (0.5)	21 (0.3)	69 (0.4%)

[a]Percentage of the number released as 2-yr-olds.

TABLE 4. Recoveries of planted lake trout in Brewer and Costello lakes of Opeongo and Simcoe stock, 1973–79.

Recipient lake	Parental stock		Totals
	Opeongo no. (%)	Simcoe no. (%)	
Brewer	19 (2.2)	7 (0.5)	26 (1.1)
Costello	15 (1.8)	10 (0.7)	25 (1.1)

TABLE 5. Comparison of returns of Lake Opeongo and Lake Simcoe individuals in 1973–76 and 1977–79. Chi-square value results from test of hypothesis that relative proportions of each stock did not change between the two time intervals. $\chi^2 = 0.04$, df = 1, $P = 0.95$.

	Lake Opeongo stock	Lake Simcoe stock
1973–76	23	7
1977–79	29	10

equally represented in the 1977 spawning run at age 6+ yr (Tables 7 and 8). After 6+ yr, trout released as yearlings were more abundant than those released at age 2, although not statistically so at $P < 0.05$ (Table 8).

Superior stock trout appeared in relatively low numbers at age 5+ (CUE of 0.07 for three plantings), but at 6+ the CUE had increased by eightfold (Table 7). Of the Superior trout aged 5+ and 6+ caught during fall 1980, 85 and 75%,

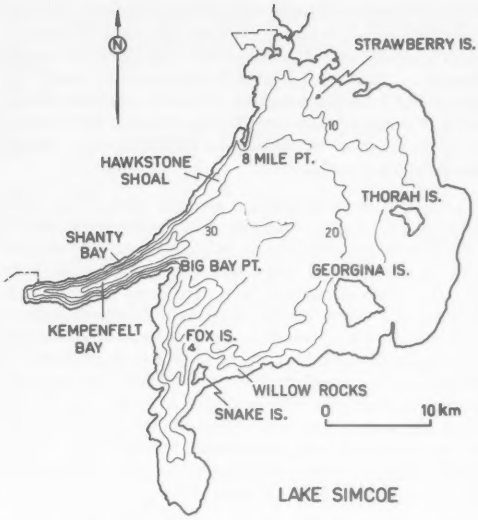

FIG. 3. Lake Simcoe showing depth in metres and geographic locations mentioned in the text.

respectively, were male (pooled $\chi^2 = 12.40$, $P < 0.01$), suggesting 7+ to be the 1st yr of major contribution to the spawning stock by the females. Under hatchery conditions at Hills Lake, Ontario, females of the Superior stock reach first maturity at 5+, but their eggs are small and of poor quality (P. Graf, OMNR, personal communication). At 6+, they yield their first major production of high quality eggs. Ovulation of the Superior stock over an 8-yr period at Hills Lake Fish Culture Station has been from October 3 to 26 at 7–9°C. Sampling in Lake Simcoe in 1978 and 1979 spanned most of October and temperatures from 2.5 to 13.5°C.

Distribution — Stocking and sampling locations for lake trout in Lake Simcoe are illustrated in Fig. 4. Detailed information on locations, dates, numbers, and catch per unit effort is given in Table 9. The general pattern that emerges is that capture of trout on the spawning shoals appears to be negatively related to shoreline distance from the release site. Of the 23 cases given in Table 9, 21 are consistent with the above interpretation. Some deviation from this pattern occurs in the Manitoba stock which was released at Fox Island in 1974 (Fig. 3), 15.5, 24.0, and 26.8 km from Georgina, Thorah, and Strawberry islands, respectively, three known lake trout spawning shoals. Recapture rates at the above shoals at 5+ and 6+ yr were 2.76, 0.48, and 1.85 fish per net night (CUE), respectively. At age 7+ (1980), CUE of the Manitoba stock was highest at Strawberry Island, the furthest site from the release location. Native trout of natural origin have consistently been found in greatest numbers at Strawberry Island and in greater or equal numbers at Thorah versus Georgina Island sites.

Dispersal pattern of lake trout during the fall spawning period does not appear to be related to age at stocking. Over a 5-yr period, significantly higher catches of Lake Simcoe stock of the 1971 year-class were made at Strawberry Island versus Georgina Island ($\chi^2 = 54.62$, $P < 0.005$), similar numbers of both age categories being caught at each respective site at ages 5+ and 6+ (Table 8). At ages 7+, 8+, and 9+, fewer trout from the 2-yr-old release category were caught, but the relative catch at the two shoals remained the same.

Patterns of spawning shoal "colonization" by lake trout of hatchery origin is illustrated in Fig. 4, with arrows indicating the general directions of the movements of trout from release sites to the shoals. Manitoba stock, which at ages 5+ and 6+ were most abundant at Georgina Island, had become uniformly distributed throughout the lake by the fall of 1980 at age 7+. In contrast, Simcoe hatchery stock has consistently been captured in greatest numbers at Strawberry Island (Table 9). Superior stock was captured in small numbers at each 1980 netting site following 1975 and 1976 releases at

TABLE 6. Relative contribution of introduced lake trout from various parental origins to the winter angling fishery on Lake Simcoe.

Stocking information					Year captured											
					1977			1978			1979			1980		
Year	No. (×1000)	Age	Location released	Origin	Age	*n*	% return[a]	Age	*n*	% return	Age	*n*	% return	Age	*n*	% return
1972	15.0	1	Kempenfelt Bay and Open Lake	Simcoe	6	4	2.2	7	3	0.6	8	1	0.1	9	0	0
1973	8.3	2	Kempenfelt Bay	Simcoe	6	4	4.0	7	3	1.1	8	0	0	9	0	0
1973	30.0	1	Kempenfelt Bay	Simcoe	5	10	2.3	6	22	1.9	7	10	2.7	8	5	0.8
1974	5.9	2	Fox Island	Simcoe												
1974	31.0	1	Fox Island	Manitoba	4	25	4.2	5	36	2.3	6	7	1.4	7	4	0.5
1975	18.2	2	Fox Island	Manitoba												
1975	15.4	1	Fox Island	Superior	3	3	1.6	4	17	3.5	5	2	1.3	6	3	1.2
1976	31.0	1	Georgina Island	Superior	2	0	0	3	2	0.2	4	4	1.3	5	8	1.6
1976	31.0	2	Georgina Island	Superior	3	0	0	4	29	2.9	5	3	0.9	6	0	0
1977	25.2	2	Georgina Island	Manitou	2	—	—	3	7	0.9	4	9	3.5	5	11	2.6
1977	74.9	1	Georgina Island	Manitou	1	—	—	2	—	—	3	0	0	4	25	2.0
1978	113.4	1	Georgina Island	Simcoe	—	—	—	1	—	—	2	—	—	3	10	0.5

[a]Actual number of fish sampled and calculated return as percentage of number released (see text for explanation).

TABLE 7. Contribution of introduced lake trout from various parental origins to the spawning population in Lake Simcoe.

Stocking information				Year captured																	
				1976				1977				1978				1979				1980	
Year[a] released	No. (×1000)	Age	Origin	Age	n[b]	Adj. n[c]	CUE[d]	Age	n	Adj. n	CUE	Age	n	Adj. n	CUE	Age	n	Adj. n	CUE	Age	n	Adj. n	CUE
1972	15.0	1	Simcoe	5	22	73	0.71	6	53	177	2.03	7	40	133	1.16	8	22	73	0.86	9	22	73	0.99
1973	8.3	2	Simcoe	5	11	66	0.64	6	30	181	2.08	7	10	60	0.52	8	6	36	0.42	9	8	48	0.65
1973	30.0	1	Simcoe	4	4	6	0.06	5	58	81	0.93	6	111	155	1.35	7	49	68	0.80	8	47	65	0.88
1974	5.9	2	Simcoe																				
1974	31.0	1	Manitoba	3	2	2	0.02	4	15	15	0.17	5	225	229	1.99	6	138	140	1.65	7	85	86	1.17
1975	18.2	2	Manitoba																				
1975	7.8	1	Superior	2	—	—	—	3	0	0	0	4	0	0	0	5	0	0	0	6	10	64	0.86
1976	31.0	1	Superior	1	—	—	—	2	—	—	—	3	0	0	0	4	0	0	0	5	8	13	0.18
1976	31.0	2	Superior	2	—	—	—	3	0	0	0	4	2	3	0.03	5	2	3	0.04	6	9	15	0.21
1977	74.9	1	Manitou					1	—	—	—	2	—	—	—	3	0	0	0	4	37	25	0.34

[a]Release locations as in Table 6.
[b]Number of fish caught.
[c]Number of fish caught, adjusted to a common stocking rate of 50 000 fish per year.
[d]Catch per net night, adjusted to common stocking rate.

Fox and Georgina Islands, whereas Lake Manitou stock released at Georgina Island in 1977 has subsequently been captured in equal numbers at Strawberry and Georgina islands. Nonnative stocks have tended to become more widely dispersed than Lake Simcoe stock. However, some individuals of all introduced stocks have dispersed widely and shoals as far as 30 km from the release sites have been visited during the spawning period.

Growth — Fork lengths are given in Table 10 for 1035 hatchery and 65 native lake trout sampled during October on Lake Simcoe spawning shoals. Hatchery trout were assigned ages on the basis of distinctive finclips and scale interpretation. Native trout have been aged using scales but only ages 5+ to 8+ have been reported, as scale interpretation of known age fish has been found by us to be repeatable within ±1 yr between these ages. Negative error in interpretation of scales increases directly with age beyond age 8. Growth rates are similar among the various stocks. At ages 5+ to 8+, the mean fork lengths for the introduced stocks are bounded by the size range of the native (naturally recruited) trout. Present growth rate is similar to that reported for native trout during the period 1954–63 (McCrimmon 1963).

Ecological Adaptations

SPAWNING MOVEMENTS

The spawning behavior and breeding structure of lake trout populations are currently being investigated in a cooperative project that involves J. MacLean, D. Cucin, J. Murdock, F. Hicks, and N. Martin of the Ontario Ministry of Natural Resources, and J. Kelso of Fisheries and Oceans Canada. In this paper, we present a preliminary analysis of the results of a test of the hypothesis that lake trout home to spawning areas (Eschmeyer 1953, 1955; Martin 1957, 1960; Loftus 1958; Rahrer 1968).

Two approaches have been used to test this hypothesis. (1) The release of numbered tags. Spawning lake trout were captured with trap nets on two spawning shoals (Lucky Strike and Pine Island) in the East Arm of Lake Opeongo (Fig. 1) between 1975 and 1979. The fish were anesthetized with MS222 and a numbered disc tag was attached with monofilament under the dorsal fin. The length, sex, and age of each fish was determined. Tagged trout were recaptured in trap nets and by anglers. (2) The release of sonic tags. In 1979, lake trout were captured with trap nets on both spawning shoals, anesthetized, and a coded ultrasonic transmitter (Smith-Root Electronics) was attached to the fish just below the dorsal fin with stainless steel wire and a surgical needle. The trout were held for 5 min to ensure they would recover and then released. They were located for ~ 2 wk after release with a receiver and hydrophone (Smith-Root Electronics). Kelso (1976) found that the effects of transmitter attachment was confined to the first 24 h.

Numbered tags were attached to 1010 lake trout during October from 1975 to 1979, including 634 from the Lucky Strike shoal and 376 from the Pine Island shoal. Adults move between basins of Lake Opeongo during the year, but only 17% of the 237 tagged fish that have been captured by anglers were caught in the North and South Arms. A total of 55

TABLE 8. Comparison of capture rates and spawning distribution of introduced lake trout of Lake Simcoe parental origin released at 1 versus 2 yr of age. ns = not significant ($P > 0.05$).

Year captured (age)	Age at release	Netting location: Strawberry Glenrest No.[a] χ^2(df)	Strawberry Glenrest CUE[b] P	Thorah No. χ^2(df)	Thorah CUE P	Georgina Willow Rocks No. χ^2(df)	Georgina Willow Rocks CUE P	Combined No. χ^2(df)	Combined CUE P
1976	1	11.0	0.61	3.0	0.10	3.0	0.10	17.0	0.22
(5+)	2	7.2	0.40	1.8	0.06	3.6	0.12	12.6	0.16
		0.90(1)	ns	0.36(1)	ns	0.05(1)	ns	1.31(3)	ns
1977	1	37.0	0.69	—		16.0	0.48	53.0	0.61
(6+)	2	41.5	0.77	—		12.5	0.38	54.1	0.62
		0.26(1)	ns			0.43(1)	ns	0.69(2)	ns
1978	1	28.0	0.77	3.0	0.08	9.0	0.21	40.0	0.35
(7+)	2	16.2	0.45	1.8	0.05	0.0	0.0	18.0	0.16
		3.15(1)	ns	0.30(1)	ns	9.0(1)	$P<0.005$	12.45(3)	$P<0.01$
1979	1	22.0	0.58	0.0		0.0		22.0	0.26
(8+)	2	10.8	0.28	0.0		0.0		10.8	0.13
		3.82(1)	$P=0.05$	0.0		0.0		3.82(3)	ns
1980	1	15.0	0.65	—		7.0	0.14	22.0	0.30
(9+)	2	12.6	0.55	—		1.8	0.04	14.4	0.11
		0.21(1)	ns			3.07(1)	ns	3.28(2)	ns
Combined	1	113.0	0.81	6.0	0.07	35.7	0.19	154.0	0.35
	2	88.3	0.63	3.6	0.04	18.0	0.10	110.0	0.25
		8.34(5)	ns	0.66(3)	ns	12.55(5)	$P<0.05$	21.55(18)	ns

[a]Number of trout caught adjusted to a common stocking rate of 15 000 per year.
[b]Catch (number of trout) per net night.

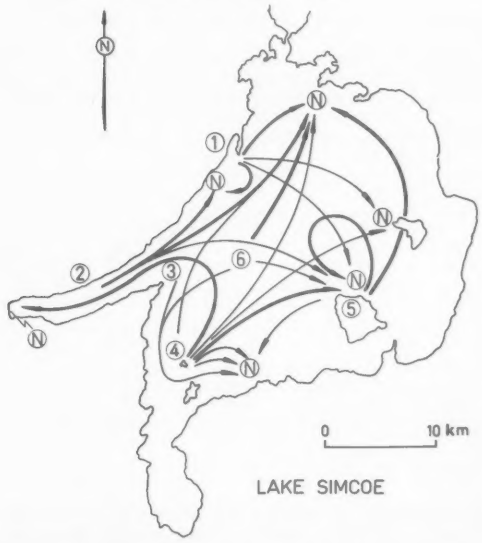

FIG. 4. Movement patterns of planted lake trout in Lake Simcoe showing the extent and general directions of travels from release locations (numbered circles) to spawning shoals (*N*) where nets operated during October and November. See the text and Table 9 for details.

tagged trout were recaptured in trap nets more than once during the same spawning period ("within year") while 194 fish were recaptured after at least 1 yr ("between years"). Recaptures of tagged trout from the two spawning shoals were analyzed to test the homing hypothesis (Table 11).

Movement patterns of males and females were different, as only 6% (2/30) of the males and over 50% (12/23) of the females moved 2.5 km between the shoals within years. A similar difference was observed between years, as 28% (29/75) of the males and 48% (43/90) of the females moved between shoals. Ages of the recaptured lake trout suggest that younger males and older females moved between shoals more than older males and younger females (Table 12).

The numbered tag data thus suggested that male lake trout home to the same spawning shoal each year and remain on that shoal throughout the spawning period, whereas females move between shoals both within and between years. Sonic tags were attached to 16 adults (10 females, 6 males) during 1979 to test this difference between sexes in movement patterns (Table 13).

The results of the sonic tag study have suggested a different pattern of spawning movements. Each individual was located between 2 and 38 times during the observation period, and both males and females moved throughout the East Arm (Fig. 5). The major difference between sexes was that some females moved further than males, as six females (numbers 3, 4, 5, 12, 13, 16) moved further than the most active male (number 5). Three females moved between Lucky Strike and Pine Island, with one female (number 3) visiting both shoals on the same evening, but no male was found on both shoals.

TABLE 9. Recapture statistics for several introduced lake trout stocks in Lake Simcoe.

Year of recapture	Netting location (net nights)	Parental origin Year released: Native ≥5+	1968–69 9+	Lake Simcoe 1969 (No. caught, CUE)[a] 8+	1972–73 5+	1973–74 4+	Clearwater Lake 1974–75 3+[b]
1976	Hawkstone (25)	23 0.92	23 0.92	7 0.28	9 0.36	2 0.08	2 0.08
	Strawberry (18)	77 4.28	28 1.56	6 0.33	15 0.83	1 0.06	0 0
	Thorah (30)	50 1.67	6 0.20	1 0.03	4 0.13	1 0.03	0 0
	Georgina (30)	11 0.37	6 0.10	0 0	5 0.17	0 0	0 0
	Combined (103)	161 1.56	63 0.61	14 0.13	33 0.32	4 0.04	0 0
1977	Strawberry Glenrest (54)	22 0.41	30 0.56	9 0.17	60 1.11	54 1.00	5 0.09
	Georgina (33)	11 0.20	2 0.06	2 0.06	23 0.70	4 0.12	10 0.30
	Combined (87)	33 0.38	32 0.37	11 0.13	83 0.95	58 0.67	15 0.17
1978	Strawberry (36)	33 0.92	19 0.53	4 0.11	37 1.03	74 2.06	82 2.28
	Thorah (37)	2 0.05	0 0	0 0	4 0.11	17 0.46	12 0.32
	Georgina (42)	12 0.29	5 0.12	1 0.02	9 0.21	20 0.48	131 3.12
	Combined (115)	47 0.41	24 0.21	5 0.04	50 0.43	111 0.97	225 1.96
1979	Strawberry (38)	20 0.53	3 0.08	3 0.08	28 0.73	44 1.16	54 1.42
	Thorah (16)	8 0.50	0 0	0 0	0 0	4 0.25	10 0.63
	Georgina (31)	5 0.16	0 0	0 0	0 0	1 0.03	74 2.39
	Combined (85)	31 0.36	3 0.04	3 0.04	28 0.33	49 0.58	138 1.62
1980	Strawberry (23)	21 0.91	0 0	0 0	22 0.96	34 1.48	31 1.35
	Georgina (30)	1 0.03	0 0	0 0	1 0.03	0 0	27 0.90
	Willow Rocks (21)	6 0.29	0 0	0 0	7 0.33	13 0.62	27 1.29
	Combined (74)	28 0.38	0 0	0 0	30 0.39	47 0.64	85 1.15
Stocking location[c]			1 and 3	2	2 and 6	2 and 4	4
No. stocked (×1000)			9 1.5	20	15 8	5.9	49.2

[a]Catch per net night.
[b]Age of various stocks in 1976.
[c]See map (Fig. 4).

Three adults left the East Arm, as two moved into Annie Bay (numbers 3, 7) and a male moved into the North Arm.

The movements of both males and females suggest that lake trout do not home each year to the same shoal. Lake trout spawn between 18:00 and 23:00 (Martin 1957) and each adult was located during 2–11 evenings. All adults were observed on at least two spawning shoals during these times, and one female (number 4) visited seven different shoals on eight evenings. Adults also appeared to visit spawning shoals during daylight, so that 65% (151/231) of all locations of tagged fish, during both day and night, were in association with known spawning shoals. Two females (numbers 4 and 16) visited a total of 10 spawning shoals during the 2 wk, while one male (number 5) visited nine shoals over 10 d of obser-

TABLE 10. Fork lengths of several introduced lake trout stocks in Lake Simcoe, Ontario, at time of capture on spawning shoals.

Origin of stock	Parental stock	Year released (age)	Age (yr) 3+	4+	5+	6+	7+	8+	9+
			Mean fork length (mm) ±Standard deviation[b] *n*						
Lake Simcoe	Native[a]	—	—	501 497–505 2	557 24 12	573 27 23	622 22 19	676 39 9	
	Wild	1972 (1)	—	—	569 72 20	569 48 53	602 32 40	638 46 22	654 33 22
	Wild	1973 (2)	—	—	562 42 11	570 32 30	608 29 10	652 24 6	641 40 8
	Wild	1973–74 (1 and 2)	—	470 453–500 3	557 52 58	580 33 111	617 37 49	661 58 47	—
Clearwater Lake, Manitoba	Wild	1974–75 (1 and 2)	491 472–510 2	518 31 15	558 32 225	601 28 138	637 33 85	—	—
Lake Superior	3rd generation domestic	1975–76 (1 and 2)	507 471–542 2	515 480–560 4	571 27 10	598 36 19	—	—	—
Lake Manitou	Wild	1977 (1 and 2)	488 465–515 2	502 22 43	—	—	—	—	—

[a]Captured during 1977–79 inclusive.
[b]Range given where $n < 5$.

TABLE 11. Recaptures of tagged lake trout on spawning shoals both within the same spawning period and between spawning periods. Chi-square values result from 2 × 2 contingency tests of the hypothesis that the movements of males and females are identical.

	Within year		Between years	
	Same shoal	Different shoal	Same shoal	Different shoal
Male	30	2	75	29
Female	11	12	47	43
	$\chi^2 = 14.87$, $P < 0.001$		$\chi^2 = 8.18$, $P < 0.01$	

vation. Thus, although females move further than males, the number of shoals they visit does not appear to differ.

Adults of both sexes moved between spawning shoals during the same evening. A total of eight such moves was observed, as one male moved 1 km at a minimum speed of 0.6 km/h and six females moved an average distance of 1 km between shoals at an average minimum speed of 3 km/h.

Two patterns of activity were observed over the period of observation. (1) Several adults moved continuously during the spawning period. For example, female number 4 moved a minimum distance of 52.9 km between October 10 and 22, visiting 10 different spawning shoals (Fig. 5a). (2) Other

TABLE 12. Movements of lake trout of different ages on two spawning shoals. Chi-square values result from 2 × 2 contingency tests of the hypothesis that the movements of young (7–9) and old (10–19) adults are identical.

Sex	Age	Within years Same shoal	Within years Different shoal	Between years Same shoal	Between years Different shoal
Male	7–9	12	1	48	22
	10–19	14	1	28	7
				$\chi^2 = 4.60$, $P < 0.05$	
Female	7–9	1	7	26	17
	10–19	9	5	22	28
		$\chi^2 = 4.23$, $P < 0.05$		$\chi^2 = 2.51$, $P > 0.1$	

TABLE 13. Summary of observations of lake trout with ultrasonic tags during October 1979.

Fish No.	Sex	Age	Tagged		No. of times located	No. of evenings located	No. of days located	Minimum distance moved (km)	No. of spawning shoals	
			Date	Site					Evenings	Total
1	M	14	Oct. 10	PI	2	2	0	—	2	2
2	M	8	Oct. 10	PI	16	5	9	16.2	3	5
3	F	8	Oct. 10	LS	32	10	13	31.8	4	5
4	F	10	Oct. 10	LS	36	8	13	52.9	7	10
5	M	8	Oct. 10	LS	25	9	10	25.1	6	9
6	F	9	Oct. 10	LS	38	7	14	42.2	5	9
7	M	19	Oct. 10	LS	11	5	7	13.3	3	4
8	M	9	Oct. 10	LS	32	8	10	24.6	4	7
9	F	9	Oct. 10	LS	25	7	11	21.6	3	5
10	F	8	Oct. 10	LS	17	6	5	21.9	2	3
11	M	—	Oct. 11	PI	22	6	10	10.2	3	4
12	F	9	Oct. 11	PI	35	8	11	40.8	5	6
13	F	9	Oct. 11	LS	32	8	13	30.2	2	5
14	F	10	Oct. 11	LS	9	4	3	7.2	3	3
15	F	9	Oct. 11	LS	28	7	9	24.3	2	6
16	F	9	Oct. 11	LS	29	7	12	40.8	6	10

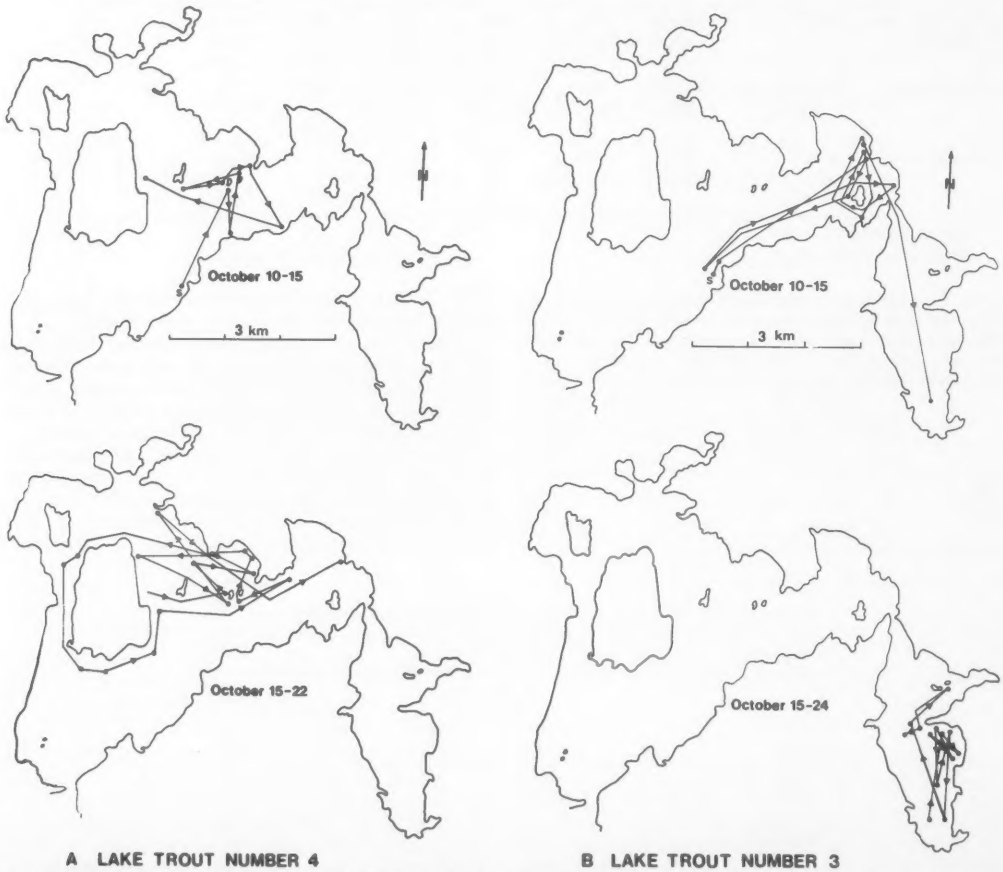

FIG. 5. Movements of two female lake trout in the East Arm of Lake Opeongo during October, 1979. Successive locations are indicated by solid points and joined by lines: (A) lake trout number 4; (B) lake trout number 3.

TABLE 14. Time of spawning of lake trout in Lake Simcoe, Ontario. Dates and temperatures bracket ranges for specific activities over years.

Decade	Years of observation	First ovulated female		Period of peak spawning activity		Spawning period
		Date	Temp. (°C)	Date	Temp. (°C)	
1950–60	9	Oct. 13–25	7.8–14.0	Oct. 16–30	8.9–13.3	Oct. 13–Nov. 1
1960–70	9	Oct. 17–25	7.8–14.4	Oct. 17–Nov. 3	8.9–14.4	Oct. 17–Nov. 4
1970–80	7	Oct. 18–Nov. 2	8.3–13.0	Oct. 21–Nov. 9	7.1–13.5	Oct. 18–Nov. 10

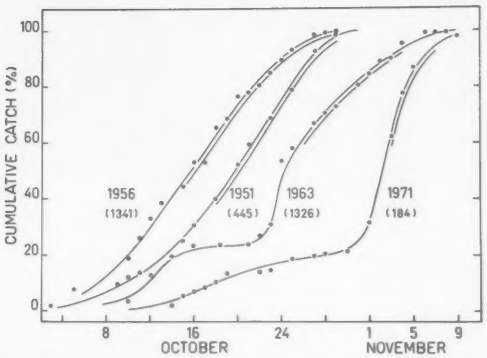

FIG. 6. Cumulative catch curves for lake trout on Lake Simcoe spawning shoals during 1951, 1956, 1963, 1971. Sample size is in parentheses; the underscored line indicates presence of ovulated females.

adults appeared to remain within one area of the lake for periods that ranged from 2 to 7 d. Female number 3 remained in the eastern end of the East Arm between October 10 and 14, visiting four spawning shoals, and moved almost 3 km on October 15 into Annie Bay, where she remained near a single shoal until October 25 (Fig. 5b). In both cases, the tagged fish appeared to move nonrandomly between shoals, and to confine their activity to some subset of all shoals.

The movements of spawning lake trout in Lake Opeongo thus suggest that neither males nor females home precisely to a single shoal each year. Both sexes visit several shoals, although males do not appear to move as far as females.

TIME OF SPAWNING

Our objective is to compare the time of arrival and reproductive status of adult lake trout of two parental origins (Lake Simcoe and Clearwater Lake, Manitoba) at known spawning shoals in Lake Simcoe. Trap nets were employed during October and November and every captured lake trout was sampled for length, age, sex, state of maturity, and finclips.

Time of spawning of lake trout in Lake Simcoe is well-known (McCrimmon 1958 and Table 14). Peak spawning activity, as judged by the presence of ripe (ovulated) females, has varied from October 16 to November 9 during the past 30 yr. Clearwater Lake lake trout (see description in Schlick 1978) are an important source of eggs for fisheries management purposes in Manitoba, with more than 1 million eggs being collected annually. Consequently, spawning time of this stock is also well-known, occurring from September 22 to October 3 at temperatures from 5.5 to 10°C (G. R. Thomas, OMNR, personal communication). Clearwater lake trout thus spawn 3–4 wk earlier and at temperatures about 3°C cooler in their home lake than native lake trout in Lake Simcoe.

Temperature has long been thought to be an important regulator of spawning time of lake trout (DeRoche 1969; Royce 1951), although McCrimmon (1958) did not find this to be so in Lake Simcoe, and clear accounts of the influence of temperature are not available. The present case offers an opportunity to examine the extent of environmental modulation of spawning time for two stocks which are normally displaced latitudinally by 9°40′ and spawn at different times and temperatures in their home lakes.

Analysis of 25 yr of lake trout spawning records for Lake Simcoe indicate that temperature during the prespawning period is correlated with time of spawning. Figure 6 illustrates the full range of variability which has been observed. Spawning has been notably delayed in the warmest years and earliest in the coldest (Table 15). Spawning of Simcoe and Clearwater lake trout stocks in Lake Simcoe has been compared within the same years to eliminate between-year thermal variations.

Sex ratios of Simcoe and Clearwater lake trout on spawning shoals in Lake Simcoe indicate a predominance of males at age 5+ (67 and 63%, respectively), but a complete reversal at age 6+ and 7+, with females comprising about 60% of the spawning run (Table 16). Both stocks appear to recruit mature males at age 5+, 1 yr earlier than the females, as is common among lake trout populations (Martin and Olver 1980).

Patterns of the spawning runs for Simcoe and Clearwater stocks during 1978 indicate that males dominate numerically during an initial phase of at least 1 wk, followed by a 6- to 8-d period when females dominate and spawning occurs (Fig. 7). Timing of the female component of the run appears to be advanced by 2–4 d for the Clearwater stock. Younger lake trout tend to spawn earlier (Martin and Olver 1980) so that the slight advancement of the Clearwater run in 1978 may reflect their initial spawning. Dates for key events during spawning (Table 17) indicate no major differences between timing of spawning for the two stocks during 1979 and 1980, when effects of first maturity were largely absent. However, the first ovulated females of the Manitoba stock appeared a few days earlier than their Simcoe counterparts in each of the 3 yr. Dates given in Table 17 have been estimated using analysis of cumulative frequency curves for each component of the spawning runs. Timing of spawning of the Clearwater stock in Lake Simcoe is similar to the native stock and, during 1978, 1979, and 1980, occurred 3–4 wk later than the parental stock in Clearwater Lake, indicating that variation in

TABLE 15. Correlation between spawning time of lake trout and mean daily surface temperature in Lake Simcoe.

	Year							
	1951		1956		1963		1971	
Date	Temp.[a]	Spawn[b]	Temp.	Spawn	Temp.	Spawn	Temp.	Spawn
Oct. 10–15	12.0	—	12.2	—	15.6	—	15.0	—
Oct. 16–20	11.4	+	12.0	—	15.1	—	14.6	—
Oct. 21–25	9.9	++	10.8	++	14.2	—	14.6	—
Oct. 26–30	8.8	—	9.3	+	14.3	+	13.6	—
Oct. 31–Nov. 4	—	—	—	—	12.2	++	12.2	++

[a]Mean daily surface temperature based on daytime observations.
[b]Intensity of spawning: (—) none, (+) active, (++) peak.

TABLE 16. Sex ratios of spawning lake trout of different parental origins in Lake Simcoe.[a]

				Males		Females		Unknown	
Origin of stock	Parental stock (year-class)	Age	No. caught	No.	%	No.	%	No.	%
Lake Simcoe	Native (1962–75)	≥5+	108	49	45.4	54	50.0	5	4.6
	Wild (1972)	5+	58	39	67.2	15	25.9	4	6.9
		6+	111	39	35.1	67	60.4	5	4.5
		7+	49	20	40.8	29	59.2	0	0
		8+	47	24	51.1	23	48.9	0	0
Clearwater Lake, Manitoba	Wild (1973)	4+	15	7	46.7	1	6.7	7	46.7
		5+	225	142	63.1	60	26.7	23	10.2
		6+	138	43	31.2	86	62.3	9	6.5
		7+	85	34	40.0	50	59.8	1	1.2

[a]Data collected during October–November, 1977–80.

spawning time, in this case, is primarily under environmental control.

Discussion

Our observations in Lakes Opeongo and Simcoe, together with studies discussed in other parts of this symposium, suggest the critical need for a stock concept for management of lake trout. Larkin's (1972) definition of stock implies that the manager must make a decision, based on a set of ecological, economic, and political constraints, about the appropriate level of biological resolution for management action. This paper attempts to develop a biological framework for a stock concept for this species.

Genetic Origin and Survival of Planted Lake Trout

The genetic origin of planted lake trout appeared to influence their survival in both Lake Opeongo and Lake Simcoe. Haskell et al. (1952) planted yearlings from Raquette Lake and Seneca Lake in Raquette Lake and reported that survival of native trout was higher. Plosila (1977) reported that lake trout of Upper Saranac Lake, a softwater lake in the Adirondacks, had a higher survival in Adirondack lakes than trout of Lake Seneca, a hardwater lake in the Finger Lakes area.

The basis for these differences in survival between stocks is not known. Plosila's (1977) results and our observations in Brewer and Costello lakes suggest that adaptations to coarse-grained features of lakes, such as seasonal temperature variation and water chemistry, are the basis for the observed differences. The movement of spawning adults between shoals in Lake Opeongo further suggests that fine-grained adaptations are less important. The similarity of growth rates of planted and natural trout and between planted stocks in both Lake Simcoe and Lake Opeongo implies that genetic adaptations to feeding and growth are not critical. Martin (1966) showed that slow-growing lake trout from Louisa Lake increased their growth rate when they were transferred to Lake Opeongo.

The experiments in Lake Opeongo, together with studies by Haskell et al. (1952) and Plosila (1977), suggest that adaptations to water chemistry may influence survival of planted lake trout. The lack of differences in survival within stocks of trout reared in hardwater and softwater hatcheries implies that physiological adaptation to the chemistry of the rearing environment is not a sufficient explanation. Plosila (1977) held equal numbers of both hardwater and softwater lake trout stocks in live cages, but he did not observe short-term differential mortality. However, the effects of genetic adaptations to water chemistry may be long-term and indirect, acting through another source of mortality such as predation.

Differential mortality of stocks appears to occur just after planting in Lake Opeongo. Pycha and King (1967) reported that survival of lake trout during the 2–3 mo after they were planted determined the relative success of plantings in Lake Superior. Plosila (1977) found that the Seneca Lake stock disappeared during the 1st yr after planting, and that planted lake trout were recovered from the stomachs of 17% of lake trout and 4% of perch. Eight newly planted lake trout were

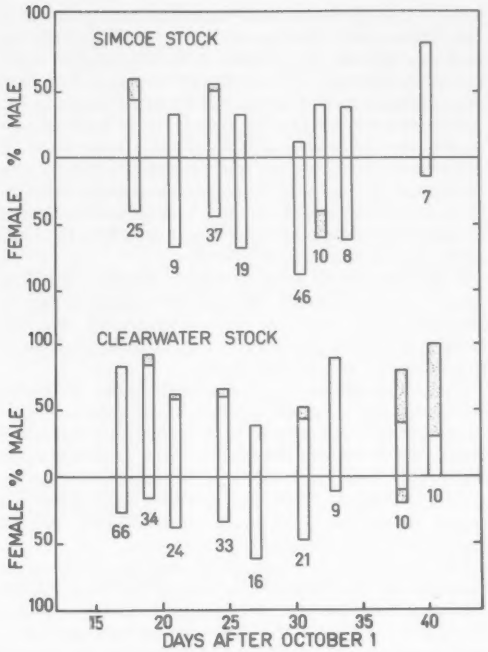

FIG. 7. Temporal patterns of spawning runs of introduced lake trout from Simcoe and Clearwater stocks. Stippled sections of bars indicate immature fish (i.e. immature males and unknown sex) above 0% line and spent females below the 0% line. .

recovered from 1560 stomachs of angled lake trout in Lake Opeongo between May and September of 1973, while only 11 lake trout, 3 of which were newly planted, had been found in 17 171 lake trout stomachs from Lake Opeongo between 1936 and 1965 (Martin 1970; Martin and Olver 1980). Currier and Shultz (1957) also report cannibalism of newly planted lake trout in Lake Minnewanka. Cannibalism may also explain the low survival of planted lake trout in Lake Opeongo. Of 112 angled lake trout examined from May to September during 1979 and 1980 in Lake Simcoe, none contained young lake trout.

In Lake Simcoe, differential mortality between stocks was not as dramatic as in Lake Opeongo. Indeed, at least one introduced stock (Manitoba) has survived as well as the native stock. Lake Superior stock survived relatively poorly, but this may be primarily related to their history of domestication. Timing of the elevated mortality suffered by the Lake Superior stock is not clear, but appears to be associated with all ages assessed to date. Lake Superior stock released as 2-yr-olds appear to have had higher mortality than those released as yearlings.

Differential mortality also occurred between yearling and 2-yr-old releases of Simcoe stock, yearling releases being more viable. This is in contrast with Buettner's (1961) study in Lake Superior, where trout 18–37 mo survived better than those 6–18 mo. These findings and those of Anderson

TABLE 17. Capture information for introduced lake trout of two parental origins during the spawning period in Lake Simcoe.

			Components of the spawning run			
				Females		
				Ovulated		Post-spawning*
Year	Parental origin	Age	Males 50%	1st	50%	1st
1978	Manitoba	5+	Oct. 19	Oct. 17	Oct. 25	Nov. 1
	Simcoe	6+	Oct. 26	Oct. 24	Oct. 30	Oct. 24
1979	Manitoba	6+	Oct. 20	Oct. 17	Oct. 22	Oct. 24
	Simcoe	7+	Oct. 17	Oct. 19	Oct. 22	Oct. 19
1980	Manitoba	7+	Oct. 20	Oct. 16	Oct. 22	Oct. 22
	Simcoe	8+	Oct. 22	Oct. 20	Oct. 22	Oct. 28

*Captured in spent condition.

(1962), Pycha and King (1967), and Plosila (1977) suggest that size, season, and age of stocking may interact to influence the survival of stocked trout.

Differences between Lakes Simcoe and Opeongo, in the survival of exotic versus native stock lake trout, suggest that survival of planted trout depends on the status of the lake trout population in the recipient lake. A higher predation rate in Lake Opeongo, which has a large, naturally reproducing trout population, may partially explain the differential success of exotic stocks in the two lakes.

Spawning distribution of hatchery trout in Lake Simcoe suggests that movements of trout of native origin are more conservative than those of exotic stocks. For example, Manitoba strain trout have become more widely distributed than natives, in spite of localized stocking in the southwest quadrant of the lake. We suggest the following testable hypotheses: (1) colonization by proximity and (2) displacement by incompatibility. In the majority of cases, recoveries of planted lake trout have been greatest at spawning shoals closest to the release sites, suggesting colonization by proximity. Colonization of nearby shoals would occur simply on the basis of random wanderings from the release sites, but it also implies the existence of some process of recognition of appropriate spawning habitat. Alternatively, colonization by proximity could be explained by some degree of homing to release sites. However, capture of nonnative trout at traditional spawning shoals in Lake Simcoe, often far from stocking sites, indicates that considerable wandering occurs and that selection of appropriate spawning habitat is occurring, by at least some stocked individuals, independent of the release site.

The second hypothesis suggests that exotic stocks may be displaced from certain shoal areas through interaction with indigenous lake trout that, on the basis of physiological or behavioral cues, identify the newcomers as intruders rather than local conspecifics. In this case, exotic stocks would colonize shoals less favored by the natives or vice versa. If the second hypothesis is true, one would expect to find some degree of segregation among the various stocks. Indeed, lake trout of natural origin and hatchery stock of Lake Simcoe parental origin have been found to predominate at Strawberry Island shoal. Additionally, 143 of 147 lake trout captured in dip nets at a marina breakwater in Kempenfelt Bay during October 1980 were Manitoba stock. The remarkable

homogeneity of the Kempenfelt Bay aggregation suggests that recognition of stock attributes may occur at the level of the individual.

The displacement by incompatibility hypothesis explains the segregation of stocks, but fails to explain why specific locations are frequented during the spawning season. Prior to the mid-1970s, spawning lake trout of native origin were widespread in Lake Simcoe (J. Lawrence, OMNR, personal communication) and the population may have been panmictic (McCrimmon 1958). The present spawning distribution, whereby native trout are more abundant in the northern areas and nonnative trout more abundant in the south, is consistent with recent stocking, abundance at spawning shoals being negatively correlated with distance from stocking sites. However, we suggest further that segregation among stocks, combined with northward expansion of range of the nonnative trout, may have resulted in restructuring of the spawning distribution of the native population.

Timing and Prespawning Movements of Lake Trout

Variation of spawning time may be an important isolating mechanism for sympatric lake trout populations (Eschmeyer 1955; Griest 1977). Evidence for inheritance of spawning time in *Salvelinus* has been reported by Berst et al. (1980). In Lake Simcoe, comparison of introduced lake trout stocks revealed that the environment was a stronger determinant of spawning time variation than inherent stock characteristics, although a small genetic component was suggested. Temperature appears to play an important role in the fine tuning of spawning time, although the combined temperature and day length effects of the latitudinal displacement involved in the Lake Simcoe study cannot be separated.

Age of maturity of Lake Superior stock in Lake Simcoe provides evidence of a genetically based stock difference. Superior stock appears to mature at age 6+ (males) and 7+ (females) in Lake Simcoe, 1 yr later than the Simcoe and Manitoba stocks. Age of release does not appear to influence the age of first maturity of the Superior stock which, under hatchery conditions, matures at 5+ and 6+ for males and females, respectively. Loftus (1958) reported 7+ as the age of first maturity for lake trout of two river-spawning stocks from the same general area of Lake Superior as the domestic Superior stock used in this study.

Preliminary observations in Lake Opeongo suggest that lake trout do not home to the same spawning shoal each year. Several studies of lake trout movements do not support this hypothesis (Martin 1960; Loftus 1958; Eschmeyer 1953), but we suggest, with the advantage of hindsight, that each of these studies contained biases which led to an underestimate of the degree of straying.

The first bias, which was a part of the above studies, was a skewed sex ratio among the tagged fish. Males predominated in all three studies, from 81% (Martin 1960) to 67–74% (Loftus 1958) of the adults. Females moved further than males between shoals in Lake Opeongo, so that a bias towards males during tagging would lead to underestimates of straying. Loftus (1958) suggested that females were less constant in choice of a spawning site.

A second bias was the distance between what were defined as distinct home areas. Spawning sites A and B, which were about 0.2 km apart in Louisa Lake, were treated as one home area (Martin 1960). If observations on these two shoals had been kept separate, the estimate of the straying rate would have trebled, from 5 to 27%. Loftus (1958) tagged fish in two rivers, which were 88 km apart, but recaptures indicated that 70% of these adults did not move more than 16 km from their tagging site. Eschmeyer (1955) defined a home range of 13 km, and assumed that any trout recaptured within this area had homed. Loftus' (1958) movement data imply that lake trout do not move far from their spawning sites, so that Eschmeyer's definition of home range may lead to an underestimate of the potential for gene flow.

A third bias would be an incomplete census of spawning sites. In all three studies, the rate of recapture of tags in succeeding years was low, even on the tagging site. The estimate of straying thus depends on the number of shoals or rivers censused as part of the study.

These three biases have undoubtedly led to an underestimate of the degree of straying and, we believe, a misunderstanding about gene flow in lake trout populations. Walch (1979) reported that displaced lake trout with radio tags would return to capture sites, and concluded that homing occurred. However, only one spawning male showed a pattern of locations which would suggest homing, and the conclusion must be considered as premature.

Two studies have argued against homing of lake trout. McCrimmon (1958) reported that only 2 of 500 tagged fish were recaptured on a shoal in Lake Simcoe, and he attributed this lack of homing to "the unusually great expanse of suitable spawning beds and similar character of the various shoals." DeRoche (1962) noted that "lake trout may migrate long distances to spawn and may not utilize the nearest available spawning area." Movements of 6.5 km between two shoals during 24 h were observed on several occasions.

Despite the observed movements between spawning shoals in Lake Opeongo, and the wide-ranging colonization of spawning shoals of introduced trout in Lake Simcoe, the evidence for distinct sympatric stocks of lake trout in Lake Superior and elsewhere is strong (Behnke 1972). This apparent contradiction may be explained by several existing hypotheses, including the following. (1) Lake trout move between spawning shoals just prior to spawning, but home to the same shoal to release eggs and sperm. The observed movements may be the result of an elaborate "proving" of the home shoal (Martin and Olver 1980). (2) Isolation-by-distance (Wright 1943; Malécot 1969) dictates the breeding structure of lake trout populations. The effects of gene flow between stocks would then be related to distance and effective population size. (3) Differences between stocks are maintained by differences in spawning time. Martin and Olver (1980) summarize differences in spawning time of stocks both within and between lakes.

In summary, we suggest that little evidence exists for the hypothesis that lake trout home to natal spawning shoals, and some combination of differences between stocks in spatial distribution and in the timing of spawning activities can explain the existence of sympatric stocks. The cohesiveness of spawning groups would be further reinforced if individual trout seek out similar individuals to spawn.

The failure of hatchery-reared lake trout to survive and reproduce is a critical concern to managers involved in reha-

bilitation or preservation of natural populations. Our results suggest that coarse-grained differences can be important to the success of introduced trout. We would also argue that the management concern for fine-scaled relations, such as homing to natal spawning areas, is not warranted at present.

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Performance of Indigenous, Exotic, and Hybrid Strains of Brook Trout (*Salvelinus fontinalis*) in Waters of the Adirondack Mountains, New York[1]

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WEBSTER, D. A., AND W. A. FLICK. 1981. Performance of indigenous, exotic, and hybrid strains of brook trout (*Salvelinus fontinalis*) in waters of the Adirondack Mountains, New York. Can. J. Fish. Aquat. Sci. 38: 1701–1707.

Eleven year-classes of wild, domestic, and wild × domestic hybrid strains of brook trout (*Salvelinus fontinalis*) were stocked in a 0.19-ha Adirondack pond. Comparative survival and growth were assessed upon drainage in early fall. Rearing native wild strains to maturity in a hatchery, or domestic strains in a natural environment, did not consistently or materially affect survival of progeny, suggesting that superior performance of wild strains was largely inherent. Interstrain hybrids of wild × domestic showed survivals equivalent to the wild parents, but hybrids of two Canadian strains gave evidence of heterosis in both survival and net yield. Supplementary observations in other waters also indicated that one strain (Assinica) may be less adaptable to Adirondack conditions than the other (Temiscamie).

Key words: brook trout, wild trout, domesticated trout, interstrain hybrid trout, survival, growth, heterosis, hybrid vigor

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Onze classes d'âge de souches sauvages, domestiques et hybrides de l'omble de fontaine (*Salvelinus fontinalis*) ont été gardées dans un étang de 0,19 ha des Adirondacks. Les taux comparatifs de survie et de croissance ont été évalués lors de la vidange de l'étang au début de l'automne. L'élevage des souches sauvages indigènes jusqu'à maturité dans une pisciculture ou de souches domestiques en milieu naturel n'a pas influé de façon significative ou matérielle sur la survie de la progéniture, ce qui porte à croire que la résistance supérieure des souches sauvages leur était en grande partie inhérente. Les hybrides ont eu un taux de survie équivalent à ceux de leurs parents sauvages, mais chez les hybrides de deux souches canadiennes, on a observé le phénomène d'hétérosis pour ce qui est de la survie et du rendement net. Les observations supplémentaires dans d'autres étangs ont montré qu'une souche (Assinica) peut être moins adaptable aux conditions des Adirondacks que l'autre (Temiscamie).

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EARLIER studies demonstrated superior survival of native Adirondack hatchery-reared strains of brook trout (*Salvelinus fontinalis*) compared with inbred domesticated lines and heterosis of an interstrain hybrid of a non-indigenous wild × domestic strain (Flick and Webster 1964, 1976). In these studies domestic and wild strains tested were produced by adults maturing in hatchery and natural environments, respectively. It was recognized that effects of strain and parental environment were confounded in initial studies and that hatchery influence on survival should be examined in the reverse of these conditions. The hybrid study cited and other data also suggested that at least one of two naturalized non-indigenous strains of brook trout (*Salvelinus fontinalis*) from the James Bay area of Quebec at times experienced poor survival in Adirondack waters, but that the hybrid Canadian × domestic gave promise for general regional stocking and for the improvement of hatchery-brood stocks. Data bearing on these points were obtained over a span of 21 years and illustrate consistency as well as variation that may be encountered in several year-classes tested in a small comparatively stable field environment. Supporting information from other larger waters has been added where appropriate to enhance the interpretation of short-term experiments reported here.

Materials and Methods

The procedures used in studies on first summer mortality and growth of trout strains were tested in Laramie Pond using procedures followed earlier (Flick and Webster 1964). This 0.19-ha pond, located in the northern Adirondack foothills

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(long 74°25′, lat 44°23′), was stocked with fingerlings in late spring and inventoried by drainage 80–150 d later. Estimation of survival in a relatively controllable natural environment eliminated need for considering additional sources of mortality such as angling, some forms of predation, and sexual maturity.

The pond was fertilized annually in 1961–64 with hay (eight bales) and superphosphate (23 kg) to increase carrying capacity. Fertilization proved counterproductive as a heavy growth of *Nitella* developed hampering fish collection and favoring the establishment of a large population of odonate naiads (Aeschnidae). These were believed responsible for a sharp increase in oversummer mortality affecting all planted groups in 1967–70. Predation on fingerlings was not observed directly, but significant losses to these invertebrates seem possible in view of experiences in bass culture (Kingsbury 1937). Whatever the cause, beginning in 1972, adult trout were overwintered in Laramie Pond and removed in early spring; coincident with this, survival of planted spring fingerlings returned to previously observed levels. Low survival in 1962 was attributed to exposure to furunculosis immediately prior to release in Laramie Pond. There was no evidence that this disease was a factor influencing survival in subsequent years. The data for 1962 and 1965–70 are not as useful for the purposes of this study, but do illustrate major perturbations on a system of otherwise relatively uniform conditions.

Trout used in these experiments were hatched and reared at the Cornell University Fishery Laboratory (1958–68 year-classes) or the Brandon Park field station (1970–79), and cultural procedures were similar for all cohorts. The Brandon facility is located ~2 km from Laramie Pond and in the same watershed. Within year-class, variations in size at stocking were usually not large and probably did not affect survival materially. Wild groups sometimes were smallest at release but gave the highest recoveries. Whenever possible, finclips used for identification were selected to minimize bias by matching right and left combinations for critical comparisons.

The strains of brook trout in these experiments, described in detail in the previously cited publications, are listed in annotated form.

Adirondack Wild Strains

Long Pond Outlet — A stunted stream trout population averaging ~15 cm located near study area. Matures age 1 to 2.

Honnedaga Lake — Three hundred and seventy-eight hectare aciditropic lake in SW Adirondacks; formerly contained trout commonly reaching 1 kg, longer lived (7–8 yr) than other native strains. Matures ages 2 to 4.

Horn Lake — Fifteen-hectare mountain top lake in SW Adirondacks. Matures age 1 to 2.

Canadian Wild Strains

Assinica Lake — Broadback River system, discharging SE James Bay, P.Q. Trout large, reaching 4–5 kg; long lived, up to 11 yr in our naturalized Adirondack population. Late maturing, ages 2 to 4. Founder stock established with 1962 year-class, but must be maintained by periodic transfers from other naturalized local populations.

Temiscamie River — Tributary of Lake Albanel, also entering SE James Bay, via Rupert River. Adirondack founder stock established with 1967 year-class and self-perpetuating. Matures ages 1 to 3.

Domestic Strains

Cortland — Propagated by United States Fish and Wildlife Service for over 50 years, also variously designated as Berlin or Nashua, NH or Wythville, VA, depending on immediate hatchery of origin. Short lived, matures ages 0 to 1.

New York — Uncertain local origin and Pennsylvania stock but propagated as inbred line for many years. In 1978 replaced with United States Fish and Wildlife Service stock from Nashua NH station. Short-lived, matures ages 0 to 1.

Results

Evidence bearing on influence of brood stock environment on survival, native Adirondack vs. Canadian strains, and relative merits of wild × domestic hybrids are listed chronologically in Table 1. Information from 1 year-class may apply to more than one of these subjects and data are extracted and discussed collectively as appropriate. Between-year comparisons are difficult to interpret but are informative after transformation to biomass produced per day per unit stocked. Performance of domestic strains also provides a measure of comparative reference between year-classes even without assumptions about uniformity of the several cohorts involved.

Influence of Parental Environment on Survival

Studies comparing field performance of wild and domesticated strains usually utilize native populations as a source of wild eggs and hatchery brood stocks as sources of domesticated eggs. In earlier survival experiments we noted the possible confounding influence of heredity with factors associated with the relative nutritional endowment in the eggs and inadvertent or natural selection in the two environments (Flick and Webster 1964). Survival-related advantages might conceivably exist in early stages, at least, where the parents matured in a natural environment. We investigated this point using progeny from wild strains reared to maturity in a hatchery and from stocked domesticated strains that matured in natural waters.

1963 year-class — The comparison included two cohorts of the Cortland domestic strain. One group had as parents age 3+ survivors of the 1960 year-class planted as fall fingerlings in Long Pond and a second was from the same brood stock strain held at the Cortland National Fish Hatchery. Oversummer survivals were 46 and 34% , respectively, indicating better field performance of the cohort from parents maturing under natural conditions (χ^2 4.23, $P < 0.5$). In this experiment, possible nutritional benefits from the eggs are con-

TABLE 1. Planting and recovery data of domestic, wild, and interstrain hybrids of brook trout, Laramie Pond, 1962–79 year-classes. Significantly different χ^2 pairs of survival values bracketed by vertical lines ($P \leq 0.05$). Mark abbreviations appropriate for finclips designated. For 1975 year-class, three additional cohorts not relevant to study stocked (total of 444, recovered 218, total wt 2.14 kg, net wt 0.97 kg).

			Planting data				Recovery data					
Year-class	Strain	Fin-clips	Date	No.	Avg length (mm)	Total wt (kg)	Date and time lapse	No.	Avg length	Net yield (kg)	Sur-vival	χ^2
1962	Domestic	LV	June 14	860	64	2.81	Oct. 10	285	122	1.45	0.33	
	Assinica	RV and Ad		643	71	2.49	118 d	135	127	−0.54	0.21	
1963	Domestic (Long)	RV	June 17	250	81	1.54	Oct. 10	114	130	0.36	0.46	
	Domestic (Cort)	LV		250	76	1.22	115 d	85	127	0.14	0.34	
	Long Pond Outlet	None		250	58	0.54		131	117	0.95	0.52	
	Honnedaga	Ad		250	61	0.64		165	114	1.22	0.66	
	LPO × Dom F_1	RV and Ad		250	74	1.09		155	130	1.32	0.62	
	Honn × Dom F_1	LV and Ad		250	69	0.91		164	130	1.68	0.66	
1964	Domestic	Ad	June 15	500	41	0.54	Oct. 2	177	122	2.22	0.35	
	East Lake (wild)	RV		500	48	0.54	109 d	349	130	6.71	0.70	
	East Lake (hatch)	LV		500	46	0.50		306	114	3.22	0.61	
1966	Domestic	Ad	June 15	498	48	0.45	Oct. 19	49	114	0.18	0.10	
	LPO (hatch)	None		497	43	0.38	126 d	201	109	1.91	0.40	
	Honnedaga (hatch)	LV		499	41	0.45		263	96	1.72	0.53	
	Honnedaga (wild)	RV		500	46	0.40		211	109	1.91	0.42	
1967	Horn Lake	None	June 16	1340	46	0.73	Sept. 21 97 d	342	101	2.22	0.26	
1968	Horn Lake	None	June 5	2000	38	0.95	Oct. 9 126 d	181	118	1.77	0.09	
1970	Domestic	RV	July 6	1003	45	0.82	Oct. 19	182	124	2.40	0.18	
	Assinica	None		990	29	0.41	106 d	204	90	0.60	0.21	ns
1973	Assinica	None	May 6	1500	51	1.70	Oct. 4 151 d	441	110	2.88	0.29	
1975	Temiscamie	RP	June 30	147	61	0.31	Sept. 17	82	93	0.28	0.56	
	Temis × Dom F_1	Ad		147	64	0.48	79 d	101	105	0.56	0.69	ns
	Temis × Dom F_1	LP		148	64	0.48		94	103	0.56	0.64	
1978	Domestic	RV	June 26	250	66	0.76	Sept. 27	111	126	1.71	0.44	
	Assinica	Ad		250	60	0.57	93 d	125	107	0.96	0.50	
	Temiscamie	LV		250	60	0.57		130	107	0.91	0.52	
	Assin × Dom F_1	LV and Ad		250	68	0.63		172	123	2.49	0.69	
	Temis × Dom F_1	RV and Ad		250	67	0.79		187	124	2.69	0.75	
1979	Assinica	Ad	June 27	300	65	0.88	Sept. 14	108	105	0.25	0.36	
	Temiscamie	LV		300	59	0.60	79 d	171	103	1.57	0.57	
	Assin × Dom F_1	LV and Ad		300	69	1.26		186	121	1.95	0.62	
	Temis × Dom F_1	RV and Ad		300	71	1.28		231	120	2.28	0.77	

founded with natural selection for survival in the parents during three seasons in Long Pond.

1964 year-class — Performance of progeny of "wild" strains reared to maturity in the hatchery environment was measured in this experiment. The three groups stocked in 1964 had these parents — *Natural East Lake* — Eggs taken from a naturalized and self-reproducing population of brook trout in East Lake (13.4 ha, 4.8-m mean depth, SW Adirondacks) in fall 1963. This pond, reclaimed in 1954, was restocked with two strains of domestic origin (Cortland and one of unknown lineage available from a local commercial hatchery) and two of wild origin (Honnedaga Lake and one of unknown antecedents available from a west-coast egg broker). The 1964 year-class theoretically represented a mixed gene pool of several postreclamation generations.

Hatchery East Lake — Hatchery-reared "wild" parents of 1962 year-class from the population above. These fish matured at age 1+ and ~28 cm in length.

Domestic — Hatchery-reared New York strain, brood stock at the New York State Fish Culture Station, Randolph. The fry were small for domestic strain and there were numerous deformed individuals.

Both cohorts of the East Lake strain were as easy to rear in the hatchery as domestic stock, and both groups were about the same size at release. Survivals of naturally produced

"wild" vs. hatchery-reared "wild" cohorts, 70 and 61%, respectively, were not significantly different. Survival in the domestic reference group at 35% was substantially lower.

1966 year-class — This experiment examined the effect of rearing two wild strains to maturity in a common hatchery environment, using parental stocks one generation removed from the original native donor stocks. The cohorts involved were the following — *Long Pond Outlet* — Hatchery-reared parents from 1964 year-class maturing in Long Pond (donor water the outlet stream population).
Honnedaga Lake — Hatchery-reared parents from 1964 year-class naturalized and maturing in Long Pond.
Honnedaga Lake — Wild parents from Honnedaga Lake.
Domestic — Hatchery-reared brood stock, Cortland strain.

All three groups with wild antecedents showed survivals substantially higher than the domestic strain, 40 to 53% vs. 10%. The Honnedaga cohort from hatchery-reared parents had significantly higher survival (11%) than those from Honnedaga wild parents (χ^2 5.7, $P < 0.02$). This seemingly anomalous result could be explained by selection within the Honnedaga hatchery group for survival in Long Pond (similar to selection for higher survival in the domestic cohort in the 1963 year-class).

The data from these three experiments were inconclusive in demonstrating deleterious effects of the cultural exposure from a single parental generation. In any event, the influence on survival was not extreme as differences within the three comparisons are only ~10%. The 1963, 1964, and 1966 experiments presented the full array of possible interpretations: (1) better survival in progeny from domestic stocks maturing in a natural environment (1963), (2) better survival in hatchery-reared wild stocks (1966), and (3) no difference (1964). The question of the influence of the maternal environment on survival would best be investigated using reciprocal crosses of sib groups reared under natural and artificial conditions.

Canadian Strains

Flick and Webster (1976) reported unexpectedly low survival between planting at age 0+ and recovery at age 1+ (15 and 6%) for Assinica and Temiscamie strains, respectively. Additional observations have supported the conclusion that fall fingerling plantings of the Assinica strain have exhibited lower survivals than Adirondack wild strains. Data on the Temiscamie strain are less certain on this point but do indicate that large differences in survival may exist between the Canadian strains.

1962 year-class — Exceptionally low survival was related to exposure of both Assinica and Domestic groups to furunculosis, and observed mortality during the 2 weeks following stocking was 27 Domestic and 244 Assinica trout. These numbers were deducted from the number actually planted for purposes of computing adjusted oversummer survivals of 33 and 21%, respectively. The experiment is of interest because it documents the unequal impact of an epidemic in nature on the two strains of trout.

1970 year-class — The 1962 experiment was repeated and both Domestic and Assinica strains again exhibited low survivals of 18 and 21%. Invertebrate predation may have contributed to the low survival.

1973 year-class — A low survival of 29% was observed with this release of Assinica strain trout.

1978–79 year-class — The 1978 cohorts of Assinica and Temiscamie strains were nearly equal in survival (about 50%) and not conspicuously better than the Domestic strain (44%). In the 1979 year-class, Assinica strain survival was substantially below Temiscamie, 36 vs. 57% (χ^2 14.2, $P < 0.01$).

Interstrain Hybrids

A wild trout stocking program is dependent on a reliable and adequate supply of eggs, and wild strains also commonly present cultural problems. Superior growth and survival in Assinica × Domestic hybrids opened the possibility of significant benefits from heterosis from adoption of a hybrid stocking program (Flick and Webster 1976). This experiment gave more promising results than observed earlier using native Adirondack × Domestic hybrids as described below.

1963 year-class — Two native Adirondack wild strains (Long Pond Outlet and Honnedaga) and Cortland Domestic strain were stocked as fall fingerlings in Long Pond in 1960 and served as parents for five cohorts of the 1963 year-class (Domestic, Long Pond Outlet, Honnedaga, Long Pond Outlet × Domestic and Honnedaga × Domestic). Survival of both hybrids was significantly higher than the Domestic (least χ^2 6.2, $P < 0.02$), but did not differ from either of the wild parents. Long Pond Outlet parental strain showed lower survival than Honnedaga (χ^2 3.9, $P < 0.05$), but the respective hybrids were about equal in survival. The net yield of the hybrids was 1.4 times greater than the wild parental strains and some 4–5 times greater than the better of the two Domestic cohorts.

1975 year-class — A replicated planting of Temiscamie × Domestic hybrids was compared with the Temiscamie parent. Survival in the hybrid cohorts of 69 and 64% was not significantly higher than the 56% observed in the wild parent, but followed the same trend shown by the 1978–79 year-classes described in the following paragraph. Net yield of the hybrids was twice that of the Temiscamie parent, due in part to greater robustness.

1978–79 year-classes — In both year-classes the Canadian hybrids exhibited significantly higher survival (19 to 26%) than the respective wild parents (least χ^2 7.4, $P < 0.01$). This was largely responsible for greater net yields of 2.6 to 3.0 times that of the Assinica and Temiscamie parental strains in 1978 and 7.8 and 1.4 times greater in 1979. Survival of Assinica hybrids was lower than Temiscamie in both year-classes, significantly so in 1979 (χ^2 4.9, $P < 0.05$). The

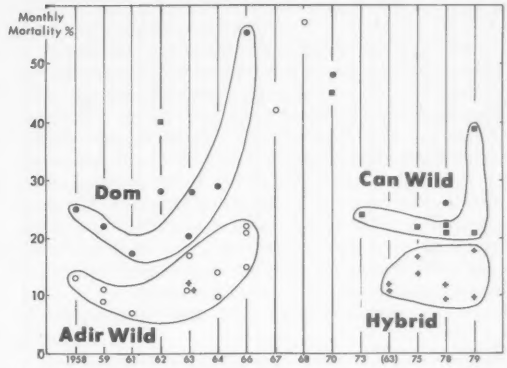

FIG. 1. Monthly natural mortality rate for several year-classes and cohorts of domestic, wild, and hybrid strains of brook trout, Laramie Pond, 1958–79. Calculated from data in Table 1. Data for 1958–61 from Flick and Webster 1964.

parental Assinica strain showed about 20% lower survival than Temiscamie in this year.

These experiments provided additional evidence of heterosis in the two Canadian hybrids. They also suggested lower first-summer survival in the Assinica strain hybrid as well as in the Assinica parent.

Discussion

Observations from all Laramie Pond experiments, transformed into monthly mortality rates and summarized chronologically in Fig. 1, provide a basis for generalizations on comparative performance. Correlation of mortality between Adirondack wild and domestic groups is apparent through time, both exhibiting decreasing mortality in the initial 3 years followed by an increase to high levels in 1963–70 ($r = 0.98$, $n = 6$, 1958–61, 1963–66), indicating common factors were closely associated with mortality in both groups.

Oversummer monthly mortality in the several Adirondack wild strains and year-classes evaluated in Laramie Pond averaged 11%, excluding the abnormally high mortality in the 1967–68 year-classes. Canadian strains show greater losses (26%), about the same as Domestic strains (23%). Although Assinica and Temiscamie strains and native Adirondack strains have not been evaluated concurrently in Laramie Pond, independent evidence indicated that non-indigenous trout sometimes had poorer field performance, and this will be examined in a separate publication.

The Assinica strain suffered significantly greater mortality than Temiscamie in the 1979 Laramie experiment, a differential also noted in other waters. As examples, stocking and ratio of recovery evaluation data for the two strains in Canachagala Lake (132 ha, avg depth 4.3 m, located SW Adirondacks), Rock Lake (77 ha, avg depth 3.9 m, SW Adirondacks), and Cranberry Pond (17 ha, avg depth 1.7 m, ~Laramie Pond coordinates) were as follows:

Water	Strain	Date planted (year-class)		Fin-clip	Length (mm)	Fish planted	Recovery/ 1000 fish planted	
							Age 1+	*Age 2+*
Canachagala Lake	Assinica	Fall 1978	(78)	RV	94	1000	0.1	1.0
	Temiscamie	Fall 1978	(78)	LV	91	1800	5.6	9.6
	Temiscamie	Spring 1979	(78)	LV and Ad	96	1232	5.1	6.5
Rock Lake	Assinica	Fall 1978	(78)	LV	78	1000	2.5	0.5
	Temiscamie	Fall 1978	(78)	Ad	76	1000	7.3	2.1
							Age 1	*Age 1+*
Cranberry Pond	Assinica	Fall 79	(79)	Ad	105	794	0.9	1.0
	Temiscamie	Fall 79	(79)	LV	98	300	7.7	8.7

The performance of interstrain hybrids using native Adirondack wild parents was not outstandingly better than the wild parental strains in the 1963 experiment in Laramie Pond. Survivors of the 1963 year-class were transferred to a nearby unpopulated Mud Pond (1.6 ha, avg depth 1.2 m) as spring yearlings in 1964 and netted intensively in autumn 1965 at age 2+ as follows:

	Stocking data		Recovery data		
Strain	Number	Length (mm)	Number	Length (mm)	%
Domestic	57	130	25	287	44
Long Pond Outlet	188	117	97	282	52
Honnedaga	164	114	115	281	70
LPO × Dom	138	130	75	298	54
Honn × Dom	146	130	98	289	67

When adjustment is made for variations in size at release, length differences between hybrid and parental groups at recapture are small (11, 2, 3, and 8 mm). As only six trout (all Honnedaga strain) were taken in the last 12 of 52 trap net days of effort, the recoveries are assumed to be the total residual population. Survival of both hybrids was nearly identical with the respective wild parents and similar to the relative pattern observed over summer in Laramie Pond. Assinica and Temiscamie hybrids consistently showed higher survival (avg 13%) than the parents in the Laramie Pond experiments and at levels equivalent to Adirondack strains.

Undetected emigration would be a source of bias in estimating natural mortality, but trout leaving Laramie Pond were captured in an inclined screen trap on the spillway. Movement was usually negligible (<10 fish) but was large in some years. Emigration in the first 3 years of study was almost exclusively of the Domestic strain and 11, 6, and 32% were trapped in 1958, 1959, and 1961. In the 1963 year-class movement was substantial in several groups, and percentages trapped of numbers stocked were:

Domestic (Long Pond)	44	Honnedaga	6
Domestic (Cortland)	26	LPO × Dom	16
Long Pond Outlet	<1	Honn × Dom	18

The catch of the two Domestic strains was again high. Both wild strains showed minimal movement and the hybrids were intermediate; over half of the emigration took place in September–October.

Keller (1974) has also documented an example of differential emigration of Assinica and Temiscamie hybrids. While only two were taken in the outlet trap the same fall as planted, 8% of Assinica and 27% of Temiscamie were captured in successive spring, fall, and spring seasons. Emigration in the preceding year-class was negligible, however. The tally of migrants in both of these studies included an unknown proportion of recycled fish as trap catches were returned to the pond without special identification. From a management standpoint, emigrants must be considered as losses.

Direct comparisons of growth rates between cohorts in a year-class as well as between year-classes are complicated by different initial sizes at stocking in Laramie Pond. Net increase in biomass (essentially net production) offers an alternative for within year-class comparisons and for conditional between year comparisons provided growth rates have not been affected by stock density. This seems true as lengths observed at the termination of the experiments (93–130 mm) were relatively uniform over a sixfold range of final populations (900–5300 fish ha^{-1}). Regression coefficients of mean lengths (or weights) on numerical population size (or biomass) at the end of each experiment were essentially 0, inferring that initial stocking levels as high as 10000 spring fingerlings ha^{-1} were not limiting oversummer growth in Laramie Pond.

Between year-class comparisons were calculated using the conventional exponential growth model to calculate the daily increment of biomass per recruit stocked in each of 34 cohorts:

$$W_0\left[e^{\frac{(\log_e W_1 - \log_e W_0}{\Delta t}} - 1\right]$$

where W_0, W_1 are initial and final weights of a cohort and Δt is the duration of the experiment in days (Fig. 2). The display reveals the generally higher biomass of hybrid cohorts, especially for Canadian strains. An experiment involving concurrent plantings of Adirondack and Canadian hybrids is desirable for controlled information on this point, but evidence available suggests that the Canadian strains may have provided the genetic diversity required for a greater expression of heterosis. Ihssen (1976) has pointed out the potential value of this kind of hybridization in fishery management.

These experiments point to the complex nature of the genetic component expressed in field performance of hatchery-reared fish as well as to genetic/environmental interactions. Wildness per se does not assure improved field performance if the unpredictable results with pure Canadian strains are typical examples. We assume that behavioral, physiological, and/or environmental factors are responsible. Naturally reproducing populations of Assinica or Temiscamie stocks have become established in Adirondack lakes where spawning conditions are suitable so adaptation is evident.

The poor survival of inbred domestic strains usually

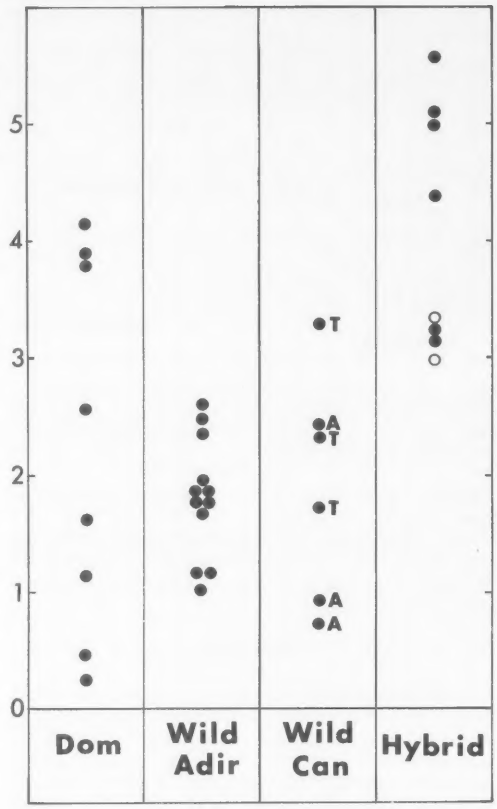

FIG. 2. Net daily increment per recruit stocked (kg^{-5}) of domestic, wild, and hybrid strains of brook trout, Laramie Pond, 1958–79. Calculated from data in Table 1 (1962, 1967–70 excluded). Data for 1958–61 from Flick and Webster 1964. Open circles, Adirondack hybrid strain, 1963 year-class. A, Assinica; T, Temiscamie.

observed under natural conditions is understandable, although explanations may be speculative. Differential performance between wild strains requires an alternative rationale since the options for intentional or inadvertent manipulations of hatchery-maintained brood stocks do not apply. A colleague, David Haskell, former foreman, New York Fish Hatchery at Rome (unpublished manuscript 1963), once commented, "Fisheries research has for years been devoted only to the [hatchery] fish that survive . . . No attention has been, or is being given to the fate of the larger groups which disappear. Can you think of another husbandry which does not consider or study the fate of those animals that 'disappear'?" Haskell's challenge is a formidable one since it involves, for the most part, assignment of causes of death without specimens in hand or confirmation by direct observations. Except where dead or moribund specimens are recovered, emigrants trapped or stomach contents of predators examined, for example,

investigators must usually resort to indirect techniques for assessing and explaining losses.

It is evident that in addition to natural causes of death, of which predation may be cited as an obvious external example, fish exposed to varying degrees of hatchery existence are subject to an additional spectrum of inherent possibilities. Mechanisms for change could be minimal in the first hatchery generation from wild parents although highly selective mortalities due to disease, metabolic stress, or nutrition could result in significant alterations in the gene pool. Cultural environments foster reduced survival in nature by protecting individuals that would otherwise rapidly succumb because they were debilitated, deformed, or behaviorally naive. However, long-term mortality factors must also operate to account for the short life span commonly characteristic of domestic strains.

Domesticated brook trout are not short-lived in all environments, striking examples of longevity being observed in fish stocked in alpine lakes of western North America. Brook trout established in the Maligne River system of Alberta from fry plantings in 1928–31 produced individuals up to 7 years of age in 1939–40 (Rawson 1941). The stock used a Pennsylvania strain in domestication since 1902 (Greene 1952). Reimers (1979) chronicled the introductory planting in Bunny Lake from which a survivor was recovered at 24 years of age and Donald et al. (1980) sampled brook trout of hatchery origin from several lakes at ages of 5–13 yr. These records, anomalous by eastern standards even for most wild populations, seem to illustrate a physiological resiliency to override selective influences of a hatchery environment.

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Structure and Affinities of Freshwater Sea Lamprey (*Petromyzon marinus*) Populations[1]

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BRUSSARD, P. F., M. C. HALL, AND J. WRIGHT. 1981. Structure and affinities of freshwater sea lamprey (*Petromyzon marinus*) populations. Can. J. Fish. Aquat. Sci. 38: 1708–1714.

We have examined genetic differentiation at 23 loci in 12 populations of sea lamprey, *Petromyzon marinus*, by means of starch gel electrophoresis. Based on two measures of overall genetic distance and two clustering methods, our analysis shows that there are three genetically distinct groups of lamprey in eastern North America: (1) anadromous populations plus those in Lake Champlain, (2) populations in Lake Erie and the upper Great Lakes, and (3) populations in Lake Ontario and three interior New York Lakes (Cayuga, Seneca, and Oneida). Analysis of population subdivision using contiguity partitions and simultaneous test procedures (STP) confirms the above conclusions and offers additional insight into the genetic structure of lamprey in this area.

Key words: sea lamprey, *Petromyzon marinus*; genetic variation, electrophoresis, population structuring

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Nous avons examiné la différenciation génétique à 23 loci dans 12 populations de grandes lamproies marines, *Petromyzon marinus*, par électrophorèse sur gel d'amidon. Notre analyse, fondée sur deux mesures de distance génétique générale et deux méthodes de groupement, démontre qu'il existe, dans l'est de l'Amérique du Nord, trois groupes génétiquement distincts de lamproies : (1) les populations anadromes plus celles du lac Champlain, (2) les populations du lac Érié et des Grands Lacs supérieurs, et (3) les populations du lac Ontario et de trois lacs intérieurs de l'État de New York (Cayuga, Seneca et Onéida). L'analyse par partages de contiguïté et procédés de tests simultanés (STP) appuient ces conclusions et ajoute à nos connaissances sur la structure génétique de la grande lamproie marine dans cette région.

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IT is usually assumed that sea lamprey (*Petromyzon marinus*) populations in the upper Great Lakes are recently derived from Lake Ontario stocks, having gained access to those waters with the opening of the Welland Canal in 1829 (Anon. 1967; Scott and Crossman 1973). However, the origin of lamprey populations in Lake Ontario, Lake Champlain, and several of the smaller interior New York lakes (Seneca, Cayuga, and Oneida) is unclear. Some or all of these may be relict populations, landlocked since early postglacial times, or they may have gained access to these waters in historical times via various branches of the New York State Barge Canal System. This matter is of more than academic interest for at least two reasons. First, if lamprey are indeed endemic, it is possible that prey species from these waters may have evolved some degree of resistance to lamprey predation. Such resistance would be useful in stocks used to repopulate areas where lamprey predation is a problem. Second, if lamprey really are endemic to certain lakes, managers may also want to reexamine a control philosophy aimed at exterminating a native species which has coexisted with the other species in these waters for over 10000 years.

Potential postglacial ancestral sources of lamprey in Ontario and the interior New York lakes were (1) the Delaware–Susquehanna drainages during the time that glacial Lake Watkins overflowed to the south via Seneca Lake, (2) one or more of the later stages in the recession of the ice front with the major drainage outlet through the Hudson–Mohawk system, and (3) the St. Lawrence River, especially during the marine incursion of the Champlain Sea. The second two possibilities would also account for the presence of lamprey in Lake Champlain.

In contrast, the Hudson River is the most likely source of recent invasion via the Erie Canal, a branch of which also

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connected with Lake Champlain. (Completion of the Chemung branch in 1833, joining the Susquehanna River and Seneca Lake, seems too recent to account for definite presence of lamprey in Lake Ontario in 1835.)

The major objective of this project was to undertake a comprehensive electrophoretic study to determine the genetic affinities of lamprey populations in waters of the northeastern United States and Canada. These would include samples from possible endemic stocks (Lake Ontario, Lake Champlain, and Cayuga, Seneca, and Oneida lakes), recently colonized stocks (Lakes Erie, Huron, Michigan, and Superior), and potential ancestral marine stocks, i.e. anadromous populations from the St. Lawrence, Susquehanna, Delaware, and Hudson rivers. Fulfillment of this goal would give insight into the current population structure of *P. marinus* in these areas and might provide critical evidence for determining the origins of the freshwater populations.

Population Structure

The amount of genetic differentiation among populations of a species, which results primarily from inbreeding and isolation, is referred to as that species' population structure (Selander 1975; Selander and Kaufman 1975). Despite the fact that information on population structure is critical to proper resource management, methods have not been available until recently for generating such data. Attempts have been made using morphological variants, but these are usually affected by an unknown number of genes and an unknown environmental component, making inferences on population structure based on such characters tentative at best. However, recently developed electrophoretic techniques for demonstrating protein variation permit the description of genotypic differences at large numbers of structural gene loci, and it is now possible to describe the population structure of almost any species in detail.

Electrophoretic variants (electromorphs) reflect simple genetic differences, and their phenotypes are codominantly expressed as bands on gels. When available, breeding data almost invariably confirm the presumed genetic model for these markers, as progeny resulting from crosses conform to the Mendelian proportions expected from the parental phenotypes. The assumption of genetic variation in species where breeding experiments are not possible is validated by criteria such as repeatability, similarity to known genetic variants in other species, and conformance of phenotypic frequencies to Hardy–Weinberg expectation.

Extensive studies of protein variation have shown spatial variation in gene frequencies among populations of most species. Animals with good dispersal abilities, such as *Drosophila*, have very similar gene frequencies throughout their ranges (e.g. Ayala et al. 1974), while species with limited mobility or pronounced homing tendencies manifest obvious geographic differentiation (e.g. Selander and Kaufman 1975). In many cases, population samples can be consistently distinguished on the basis of phenotype frequency differences or by the presence of unique variants, and such techniques have been used with considerable success in the genetic characterization of fish stocks. For example, trout and salmon populations in the Pacific Northwest have been investigated intensively using electrophoretic techniques by workers at the Northwest Fisheries Center (reviewed by Utter et al. 1976). Franzin and Clayton (1977) were able to determine postglacial routes of gene flow among western Canadian lake whitefish (*Coregonus clupeaformis*) populations by using electrophoretic markers, and these authors then related the biochemical data to the glacial refugia in which the whitefish are believed to have survived the Wisconsin glaciation. Numerous other examples of the application of biochemical techniques to biogeographical problems can be found in the recent literature.

The success of these methods for determining population affinities results from the fact that electrophoretically detectable genetic differentiation begins to accumulate in subdivided populations as soon as their gene pools become isolated. These differences result from a combination of various stochastic (founder effects, "bottlenecks," and drift) and deterministic (selective) factors. In the absence of gene flow, the rates of divergence in electrophoretic characters seem to be reasonably time-dependent (Wilson et al. 1977), and genetic distances among well-isolated contemporary populations, calculated from electrophoretic data, tend to reflect the histories of the populations. These histories not only include patterns of derivation from common stocks but may also reflect the nature of colonization events and the results of low population size.

Methods and Materials

Ammocoetes were obtained by electroshocking 11 localities from April to September, 1979, and June to August, 1980. In addition, transformers and adult lampreys were obtained from the fish weir at Cayuga Inlet, Cayuga Lake, New York, in April, 1979, and adult lampreys were obtained from the Connecticut River in June, 1980. Specimens were transported live to the laboratory and then immediately frozen at −80°C.

Protein variation was studied in both muscle and liver tissues. In preparation for electrophoresis the head, gut, skin, and notochord were removed. Animals less than 50 mm in length were ground whole. Liver and muscle were minced in equivalent volumes of grinding buffer (0.01 M Tris, 0.001 M EDTA, 5×10^{-5} M NADP, pH adjusted to 7.0 with HCl) and allowed to soak for 30 min. Following centrifugation for 20 min at 25000 g at 0–5°C, the clear supernatant was removed. Tissue extracts were stored at −80°C and most samples were electrophoresed within 2–3 wk.

The electrophoretic apparatus, gel and electrode buffers, and staining procedures used in this study were similar to those described by Selander et al. (1971), with the following exceptions: three other buffer systems were also used, "Tris–Whitt" (Whitt 1970), "ASAC" (Avise et al. 1975), and "OM" (O'Brien and MacIntyre 1969). Because of a recent change in the properties of Electrostarch, we found it necessary to mix it with Sigma starch (Sigma Chemical Company, St. Louis, Missouri 63178) for satisfactory results. For gels made with Selander's buffer No. 2, 30 g Electrostarch was combined with 17 g Sigma starch; all other systems worked well with 37 g Electrostarch: 10 g Sigma starch.

Initially a survey was conducted to determine which enzyme loci could be resolved with our techniques. Twenty-eight different enzyme assays were tested on all 12 buffer

systems (Selander's 1–9, Tris–Whitt, ASAC, and OM). A side-by-side comparison of ammocoetes, transformers, and adults from the same collecting site was carried out to determine if any ontogenetic differences exist.

Genotype frequencies were obtained by direct count from the electrophoretic phenotypes on the gels. Expected genotype frequencies under Hardy–Weinberg equilibrium were calculated using Levene's (1949) formula, and these were compared with observed frequencies by a χ^2-test for goodness of fit. Measures of between-population genetic similarity and distance were calculated using Rogers' (1972) and Nei's (1972) methods. To visualize the genetic affinities of the 12 populations, these distance measures were used to construct UPGMA phenographs (Sneath and Sokal 1973) and minimum length Wagner trees (Farris 1972). Geographical partitioning of the populations into internally homogeneous sets was done by modifications of a procedure suggested by Gabriel and Sokal (1969) and Pielou (1979). The entire area from which the samples had been obtained was subdivided into geographically connected subareas, based on water connections past and present. This information was obtained primarily from Whitford (1906) and USDA (1970). Then, the 12 samples were combined into internally homogeneous subpopulations based on the homogeneity of the observed allelic frequency distributions (STP procedure; Sokal and Rohlf 1969, p. 582).

Results

Our current understanding of protein variation in *Petromyzon marinus* is based on 775 ammocoetes collected from 11 localities as follows: 127 from Cayuga Inlet, Cayuga Lake; 65 from Fish Creek, Oneida Lake; 114 from Little Sandy Creek, Lake Ontario; 36 from Oquaga Creek, Delaware River; 71 from Bouchouxville Creek, Delaware River; 106 from Putnam Creek, Lake Champlain; 53 from Catherine Creek, Seneca Lake; 31 from Roeliff Jansen Kill, Hudson River; 30 from Nebagamon River, Lake Superior; 38 from Crooked Creek, Lake Erie; 104 from Cattaraugus Creek, Lake Erie; and from 60 transformers and 46 adult lampreys from Cayuga Inlet, Cayuga Lake, and 64 adult lampreys from the Connecticut River.

We have now analyzed variation in 18 proteins, presumably encoded by 23 loci, in all of these individuals. In the following account loci are numbered and alleles designated in order of their decreasing anodal mobility. The loci examined and the buffer systems used are esterase (EST) and general protein (GP), both on Tris-hydrochloric acid buffer (Selander et al. 1971, buffer 1); alcohol dehydrogenase (ADH), peroxidase, two loci (PER-1, PER-2), and phosphohexose isomerase, two loci (PHI-1, PHI-2), all with discontinuous Tris-citrate buffer (buffer 3); xanthine dehydrogenase (XDH), α-glycerophosphate dehydrogenase (α-GPDH), and phosphoglucomutase (PGM-2), all with continuous Tris-citrate buffer (buffer 5); glutamate dehydrogenase (GDH) with Tris-versene-borate buffer (buffer 6); lactate dehydrogenase (LDH), and octanol dehydrogenase (ODH), both with phosphate buffer (buffer 7); glyceraldehyde-3-phosphate dehydrogenase (G-3-PD) and malic enzyme (ME), both with Tris-maleate buffer (buffer 9); malate dehydrogenase, two loci (MDH-1, MDH-2), glucose-6-phosphate dehydrogenase (G-6-PD), 6-phosphogluconic dehydrogenase (6-PGD), and phosphoglucomutase (PGM-1), all with "Tris–Whitt" (Whitt 1970); and isocitrate dehydrogenase, two loci (IDH-1, IDH-2), and glutamate oxaloacetate transaminase (GOT), all on ASAC (Avise et al. 1975).

Of the preceding loci, five (α-GPDH, PHI-1, PGM-1, PGM-2, and MDH-2) proved to be polymorphic in most populations. IDH-1 was also found to be slightly polymorphic, as evidenced by several heterozygote phenotypes from the Delaware, Hudson, and Connecticut River (anadromous) populations. MDH-2 and α-GPDH are structural dimers; the heterozygotes show three bands. PGM-1 and PGM-2 are monomeric with two-banded heterozygotes. PHI and IDH homozygotes are normally expressed as three-banded phenotypes with the most anodal and most cathodal band representing homodimeric products of two loci. A band of intermediate mobility represents the heterodimer. Allelic variants at either locus result in multi-banded phenotypes representing the various possible homo- and hetero-dimeric combinations. These electrophoretic patterns are consistent with their probable homologues in other fishes.

Comparisons of ammocoetes, transformers, and adults revealed no ontogenetic changes except for slight mobility shifts between ammocoetes versus transformers and adults at both the PER-1 and PER-2 loci. It is presently unknown whether these changes result from different loci being active at different stages of the life cycle or from posttranslational changes in the proteins themselves, although the latter explanation seems most likely.

α-GPDH had two common alleles, α-GPDH^a and α-GPDH^b, both of which were present in all the samples. PHI-1^b was the common allele at that locus, while PHI-1^a occurred in low frequencies in most populations except for Oneida Lake where it reached a frequency of 0.32. It was missing in our sample from Lake Superior. PHI-1^c also occurred in low frequencies in most populations, but was missing from Seneca Lake and Lake Champlain. PHI-1$^{a'}$ was observed once as a heterozygote in the Connecticut River sample. Both PGM-1^a and PGM-1^b were present in varying frequency in all populations examined. PGM-2^a was missing from Oquaga Creek as well as from Seneca Lake, but has reached a relatively high frequency of 0.25 in Lake Superior and Lake Erie. PGM-2^c is a rare variant found only in the anadromous samples. MDH-2^b was fixed in Seneca Lake and was the most common allele in all other samples. MDH-2^a, when present, varied in frequency from 0.01 to 0.27. These data are summarized in Table 1.

The remaining 17 loci were monomorphic and showed no evidence of intra- or inter-population variability. Overall heterozygosity of *P. marinus* averaged about 6%, a value similar to that reported for most other fishes (e.g. Avise and Ayala 1976).

Four of 58 comparisons of observed and expected genotypic proportions deviated from Hardy–Weinberg equilibrium, one at the 0.01 significance level and three at the 0.05 level. In each case the deviation was accompanied by a substantial deficiency of heterozygotes. The most reasonable explanation for this is probably a Wahlund effect from combining year-classes, as all ammocoetes collected at a site (ranging from perhaps 2–6 or more years old) were pooled for our sample.

We used two measures of genetic distance and two

TABLE 1. Allele frequencies and sample sizes (*N*) at the polymorphic loci for 12 populations of *P. marinus*.*

	CAY	ONI	ONT	SEN	BXC	OQC	CHA	HUD	SUP	CRC	CAC	CON
GPDH[a]	0.58	0.61	0.54	0.64	0.40	0.32	0.27	0.29	0.25	0.43	0.45	0.32
GPDH[b]	0.42	0.39	0.46	0.36	0.60	0.68	0.73	0.71	0.75	0.57	0.55	0.68
N	50	36	49	22	57	30	99	31	30	38	91	64
PHI-1[a']	0	0	0	0	0	0	0	0	0	0	0	0.01
PHI-1[a]	0.15	0.32	0.14	0.19	0.01	0.10	0.11	0.02	0	0.03	0.03	0.02
PHI-1[b]	0.83	0.68	0.85	0.81	0.94	0.87	0.89	0.94	0.98	0.94	0.96	0.91
PHI-1[c]	0.02	0.01	0.01	0	0.05	0.03	0	0.05	0.02	0.03	0.01	0.06
N	108	65	111	53	71	36	106	31	30	38	104	64
PGM-1[a]	0.75	0.67	0.56	0.58	0.84	0.88	0.73	0.84	0.48	0.49	0.43	0.86
PGM-1[b]	0.25	0.33	0.44	0.42	0.16	0.12	0.27	0.16	0.52	0.51	0.57	0.14
N	71	60	94	49	64	34	103	49	30	38	104	63
PGM-2[a]	0.04	0.03	0.07	0	0.04	0	0.02	0.05	0.25	0.25	0.36	0.01
PGM-2[b]	0.96	0.97	0.93	1.00	0.94	0.99	0.98	0.93	0.75	0.75	0.64	0.97
PGM-2[c]	0	0	0	0	0.02	0.01	0	0.02	0	0	0	0.02
N	117	66	113	53	71	36	36	31	30	38	104	64
MDH-2[a]	0.05	0.02	0.14	0	0.15	0.19	0.01	0.27	0.20	0.12	0.16	0.19
MDH-2[b]	0.95	0.98	0.86	1.00	0.85	0.81	0.99	0.73	0.80	0.88	0.84	0.81
N	101	61	100	52	70	34	106	31	30	38	103	64

*Locality abbreviations are as follows: CAY, Cayuga Lake; ONI, Oneida Lake; ONT, Lake Ontario; SEN, Seneca Lake; BXC, Bouchouxville Creek; OQC, Oquaga Creek; CHA, Lake Champlain; HUD, Hudson River; SUP, Lake Superior; CRC, Crooked Creek; CAC, Cattaraugus Creek; CON, Connecticut River.

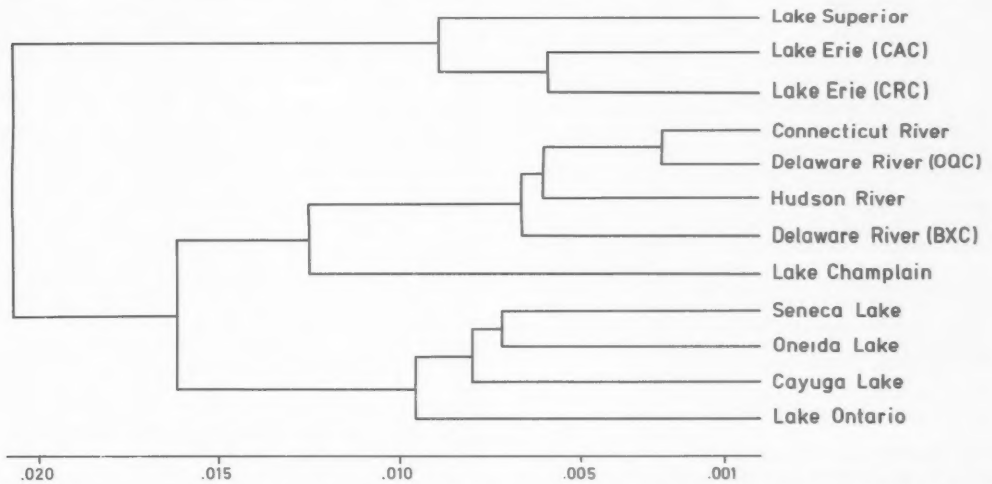

FIG. 1. Dendrogram resulting from Rogers' measure of genetic distances and UPGMA clustering technique, polymorphic loci only, on 12 populations of *P. marinus*.

clustering methods to assess the overall genetic relatedness among these populations. Both Nei's (1972) and Rogers' (1972) distance produced identical dendrograms when clustered by UPGMA (Sneath and Sokal 1973). Rogers' measure of genetic distance combined with a minimum length Wagner procedure (Farris 1972) produced a tree which was virtually identical with UPGMA.The only discrepancy between the two involved the affinities of the two Delaware River populations and the Hudson River population. Figure 1 shows the dendrogram resulting from Rogers' D and UPGMA.

Simultaneous test procedures for heterogeneity of allele frequencies (STP; Sokal and Rohlf 1969, p. 582) indicated that allele frequencies at every polymorphic locus were significantly different among various groups of populations. All the anadromous samples (CON, BXC, OQC, HUD) were homogeneous at all loci, as were the Lake Erie samples (CAC, CRC). All other populations showed statistically significant frequency differences at one or more loci. The results of this analysis and the contiguity partitioning are shown in Fig. 2.

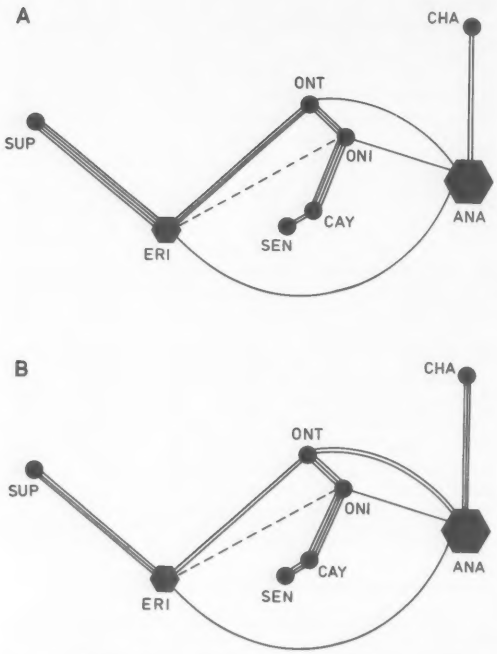

FIG. 2. Population structure of *P. marinus*. A. Genetic continuity based upon *G*-tests for heterogeneity of allele frequencies at five polymorphic loci among geographically contiguous populations. Broken line means significant heterogeneity at all five loci; single line, significant heterogeneity at four loci; double line, significant heterogeneity at three loci; triple line, significant heterogeneity at two loci; quadruple line, significant heterogeneity at one locus. B. Continuity based on Rogers' coefficient of genetic similarity using allelic frequency data from the five polymorphic loci. Broken line means similarity coefficient of 0.79−0.81; single line, 0.82−0.85; double line, 0.86−0.89; triple line, 0.90−0.93; quadruple line, 0.94 or greater. In both A and B increasing line thickness indicates increasing genetic continuity. ANA = all anadromous populations, ERI = both Lake Erie populations. All other abbreviations as in Table 1.

Discussion

We had two major objectives when we began this study. The first concerned the historical biogeography of sea lamprey populations in Lake Ontario, Lake Champlain, the Finger Lakes, and Oneida Lake. Specifically, we wanted to know whether lampreys entered these waters in historical times via the canal systems, or whether some or all of them were relict populations, isolated since the last glacial retreat. The second objective was to define the current structure of sea lamprey populations in the study area and to look for any evidence of gene flow between major population units or for evidence of substructuring within any of these waters.

At this point we have had only limited success with the former goal and somewhat more with the latter. Our current understanding of the genetic relationships among lamprey populations, based on patterns of variation at 23 loci, indicates that there are three major groups of populations in eastern North America (Fig. 1). The Delaware, Connecticut, and Hudson River populations represent anadromous stocks, and these seem to show as much differentiation among tributary creeks in the Delaware River as they do between the major river systems. The Lake Champlain population is closely related to the anadromous stock. The second major cluster includes Lake Ontario and the interior New York lakes (Seneca, Cayuga, and Oneida), and the third consists of the samples from Lake Erie and Lake Superior.

Although this pattern is clearly consistent with the geography of the region, interpreting the history of these populations from these data alone is not altogether straightforward. For this kind of study the assumption is usually made that allozymes behave as essentially neutral markers of genetic continuity or discontinuity, and that the allelic composition of any derived population will reflect primarily its ancestral source and the extent of gene flow from neighboring populations. These assumptions are probably true in general, and electrophoresis has proved to be a powerful tool for analyzing both population structure and history (e.g. Brussard 1975). Nevertheless, allozyme frequencies in any population are potentially influenced by several other confounding factors. First, the type of event leading to the population's origin can have some influence. The amount of genetic information present in a derived population will be smaller if it arose from a few colonizing individuals rather than from the isolation of a large segment of the ancestral population; furthermore, if the derived population remains small for several generations after its founding, many alleles will be lost and others will drift to abnormally high frequencies. Second, previous episodes of gene flow can have large effects on the genetic composition of contemporary populations. For neutral or nearly neutral alleles, just a trickle of gene flow can restore lost alleles and erase differences resulting from previous events. Third, local selection pressures may have some effects as well. Selection can maintain allelic differences in the face of considerable gene flow, provided that the selective pressures are strong enough. While there is little evidence to suggest that local selection pressures exert a powerful influence on most allozyme frequencies, slight deviations from expected genotypic proportions or minor frequency shifts at some loci may indicate the effects of selection (e.g. Koehn and Williams 1978). Furthermore, it is even possible that genetic divergence in some electrophoretic characters may depend on a synergistic relationship between selection and founder effects to a greater degree than is generally suspected (Baverstock et al. 1979). When a small isolate splits off from a parent population it may be free to undergo a "peak shift" (Wright 1931, 1980), or even a mild "genetic revolution" (Carson 1975) resulting in a general realignment of equilibrium allele frequencies.

The genetic structure of the *P. marinus* populations we have examined may have been affected by a combination of several of the factors mentioned above. The genetic distances among these populations are small, and result from slight, but generally significant, differences in allelic frequencies and from the presence or absence of a few rare alleles. No locus is fixed for alternate alleles in different populations; no alleles are unique to any one population; and in most cases the common allele at a locus in one population is the common

allele in all others. The average Nei distance among all *P. marinus* populations is 0.008; an equivalent level of differentiations has been observed by Merritt et al. (1978) in populations of dace, *Rhinichthys cataractae*, within the Connecticut River drainage.

Because we cannot preclude the effects of selection working on at least some loci, and because we cannot discount the possibilities of previous gene flow occurring among some of these populations, any interpretation of the history of lamprey colonization in this region based on genetic distance data must be tempered by some subjective judgments. Nevertheless, the contiguity diagrams in Fig. 2 enable us to examine these data more closely and within a geographical perspective. In this figure all contiguous populations which had no significant allele frequency differences at any loci (i.e. all anadromous samples, both Lake Erie samples) are combined. Examination of Fig. 2 leads to the following observations. First, the close relationship between the Lake Champlain population and the anadromous stock may indicate that colonization of Lake Champlain occurred as a result of postglacial incursion of the Champlain Sea, or it may indicate a recent colonization via the Champlain canal from the Hudson River. Significant gene flow between Lake Champlain populations and those in the Hudson River cannot be discounted.

Second, Lake Ontario seems to be the most likely source for the colonization of Lake Erie, rather than the Hudson River via the Erie Canal, as is occasionally suggested (T. M. Jolliff personal communication). The moderately large degree of genetic differentiation between the Ontario and Erie populations may have resulted from a rather substantial bottleneck during the colonization period.

Third, while there is certainly substantial differentiation between the anadromous populations and those in Lake Ontario, Oneida, and the Finger Lakes, the data on hand cannot unambiguously distinguish between endemicity for those populations or a more recent arrival. It is certainly possible that bottleneck effects could also have been operative in the colonization of Lake Ontario. On the other hand, positive evidence of the presence of lamprey in Lake Ontario in 1835 (Lark 1973) may provide additional evidence for endemicity, since it is unlikely that a small founder population from Hudson River stocks would have invaded, differentiated, and proliferated in the 11 years following the completion of the water connection in 1824–25. The Erie colonization poses no such time constraints, since the approximately 100 years between the completion of the Welland Canal and the recorded appearance of *P. marinus* in Lake Erie (Applegate 1950) should have provided ample time for considerable genetic differentiation to occur. Lake Erie is not particularly favorable lamprey habitat, and it is quite possible that a small colonizing population existed at a very low level there during the intervening century. This would have allowed the PGM-1^b and PGM-2^a alleles to drift to a relatively high frequency and would account for the apparent loss of the PHI-1^a allele. Lake Superior is clearly genetically very similar to Lake Erie. It was the last of the upper Great Lakes to be colonized, and as such it may represent the end of a cline of differentiation in those waters.

Fourth, there is obviously substantial similarity among the Lake Ontario and interior New York populations. Whether this similarity results from colonization from a single stock, either at the close of the Pleistocene or more recently, from gene flow among these populations, or both, is unknown, although scattered historical data tend to support endemicity (D. Webster unpublished data). There may be substantial migration among these populations as well, since there are reports of lamprey in several tributary streams in the Seneca–Oneida–Oswego River systems, which connect these lakes (D. Webster personal communication). The relative distinctiveness of Lake Ontario from Oneida Lake is also worthy of mention. If Oneida Lake contributes to the Lake Ontario population by downstream drift of transforming larvae as has been suggested by some workers (Webster 1979), this contribution, in terms of gene flow at least, may be rather small, provided, of course, that our sample is typical of the lake as a whole.

These data have provided us with a good general understanding of lamprey population structure in this region. However, a resolution of the endemicity issue and a clarification of certain finer details of this pattern will depend on additional data. Samples from key areas are currently being analyzed, and these should enhance our results substantially and facilitate the interpretation of these rather intriguing data.

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Management Implications for Different Genetic Stocks of Largemouth Bass (*Micropterus salmoides*) in the United States[1]

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PHILIPP, D. P., W. F. CHILDERS, AND G. S. WHITT. 1981. Management implications for different genetic stocks of largemouth bass (*Micropterus salmoides*) in the United States. Can. J. Fish. Aquat. Sci. 38: 1715–1723.

Genetic differences exist among 90 largemouth bass (*Micropterus salmoides*) populations from different geographic regions of the United States. Genetic variation at 28 loci was determined through the use of vertical starch gel electrophoretic analyses. Allelic polymorphism was observed at 16 of these loci. Marked differences in allele frequencies at six of these loci exist among the populations. Distinct north–south clinal distributions of the alleles at the *MDH-B*, *SOD-A*, *IDH-B*, and *AAT-B* loci suggest a possible involvement of the associated enzymes in the thermal tolerance/preference limits for this species.

We conclude that one or more of these enzymes may be directly involved in temperature tolerance/preference or indirectly associated with temperature-related effects. In either instance, selection (if occurring) may be acting upon the enzyme locus or genes closely linked to it. Through a combination of ecological and genetic principles, it is becoming increasingly feasible to select or construct specific populations of marine or freshwater fish optimally suited for specific environments. Fisheries management programs would benefit from the application of these principles. Multidisciplinary approaches of this nature are essential to maximize the successful conservation and management of our natural resources.

Key words: largemouth bass, allele, loci, polymorphism, selection, population

PHILIPP, D. P., W. F. CHILDERS, AND G. S. WHITT. 1981. Management implications for different genetic stocks of largemouth bass (*Micropterus salmoides*) in the United States. Can. J. Fish. Aquat. Sci. 38: 1715–1723.

Il existe des différences génétiques parmi 90 populations d'achigans à grande bouche (*Micropterus salmoides*) de différentes régions des États-Unis. Des analyses électrophorétiques sur gel d'amidon vertical ont permis de déterminer la variation génétique à 28 loci. On a observé un polymorphisme allélique à 16 de ces loci. Il y a parmi les populations des différences marquées de fréquences d'allèles à six des loci. On observe un net gradient nord-sud des allèles aux loci *MDH-B*, *SOD-A*, *IDH-B* et *AAT-B*. Cela indiquerait que les enzymes associés sont possiblement impliqués dans les limites de tolérance/préférence thermique de cette espèce.

Nous concluons qu'un ou plusieurs de ces enzymes peuvent être directement impliqués dans la tolérance/préférence thermique ou indirectement associés à des effets liés à la température. Dans chaque cas, la sélection (si elle se produit) peut agir sur le locus des enzymes ou sur les gènes qui lui sont étroitement associés. Grâce à une combinaison de principes écologiques et génétiques, il devient de plus en plus faisable de choisir ou de construire des

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populations particulières de poissons marins ou dulçaquicoles convenant le mieux à des environnements spécifiques. La gestion des pêches pourrait bénéficier de l'application de ces principes. Des approches multidisciplinaires de cette nature sont essentielles au succès de la conservation et de la gestion de nos ressources naturelles.

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ONE of the most significant selective pressures exerted upon poikilothermic species is environmental temperature (Somero 1969; Gibbons and Sharitz 1974). Species of North American freshwater fishes can exist over a range of temporal and spatial variation in thermal regimes. Through natural selection specific populations become genetically adapted to their specific thermal environments (Berry 1971; Holland et al. 1974; Ryman and Stahl 1980). A species which is distributed over a wide range of thermal environments might be expected to consist of populations genetically tailored for a variety of different thermal regimes. For example, populations from the northern extremes of the range would be expected to be better suited for colder temperatures than populations located in the southern portions of the range. These physiological differences are often the result of long-term natural selection rather than the result of short-term temperature acclimatization (Berry 1971; Holland et al. 1974). As a result, the genetic composition of the individuals and the populations as a whole from different regions would be expected to be different.

Identifying these genetic differences and utilizing this variability becomes very important for the management of such broadly distributed species. For example, if individuals are propagated in a hatchery environment for subsequent stocking into natural environments, it becomes imperative that the brood stock be of an appropriate genetic composition for the environments in which the offspring are to be released. However, undesirable inbreeding, which reduces genetic variability, must be avoided as well (Kincaid 1976; Allendorf and Utter 1979; Ryman and Stahl 1980). Placing individuals of inappropriate genetic composition into existing environments would not only be an inefficient use of the resource, but could even prove to be detrimental to an existing population of that species through the introduction of deleterious alleles (Hoyt 1974; Krueger and Menzel 1979). Conversely, imposing an inappropriate environment upon an existing population may also prove to be inefficient or even detrimental (Berry 1971; Coutant 1975a, b). For example, the addition of heated effluent to a body of water may create an environment which could be better utilized by individuals from a more southern genetic stock (Gibbons and Sharitz 1974). Once an environment is so altered, the ability of the existing population to survive and adapt to these new conditions would depend upon the physiological flexibility of its members, which is determined primarily by their genetic composition (Berry 1971; Low and Somero 1976; Shaklee et al. 1977). Therefore, genetic manipulation of the population prior to or concomitant with the environmental alteration might temper subsequent detrimental effects. Our knowledge of fish biochemical and ecological genetics is now reaching the point where such genetic manipulations of fish populations are becoming feasible (Larkin 1978; Silvert 1978; Moav et al. 1978).

The largemouth bass, *Micropterus salmoides*, is one of the most widely distributed species of fish in North America. Originally, its range consisted of the southern Mississippi River drainage plus the mid-Atlantic and southeastern states (MacCrimmon and Robbins 1975). However, the largemouth bass is also one of the most highly managed species of fish in North America. As such, it has probably been stocked into almost every body of water in which it could possibly survive. As a result, the current range of the largemouth bass consists of virtually the entire United States, parts of Mexico and southern Canada, as well as many countries outside North America (MacCrimmon and Robbins 1975). Furthermore, during the past 100 yr, many existing bodies of water have been frequently restocked with hatchery-reared largemouth bass. In many cases, these supplementally stocked largemouth bass were produced in a hatchery located in quite a different geographic region of the country. The genetic composition of the supplementally stocked largemouth bass may have been quite dissimilar to the largemouth bass already existing in the area. Any transient "heterotic advantage" of the progeny is outweighed by the introduction of less-adapted alleles. The reduced fitness and survival of these supplementally stocked largemouth bass may have resulted in a great deal of wasted effort and ineffective use of this important natural resource.

Because of existing management programs for largemouth bass it is crucial that we better understand the degree of genetic differentiation of existing largemouth bass populations and how this differentiation relates to the fitness of each population for the specific environment which it inhabits (Koehn 1970; Merritt 1972; Avise and Smith 1974; Childers 1975; Hjorth and Simonsen 1975; Powers and Place 1978; Place and Powers 1979). Specifically, the present report considers the extent of genetic variation among largemouth bass populations distributed throughout the United States. We will discuss how specific genetic markers can be used in designing future management programs for largemouth bass. We hope that the application of our biochemical and ecological genetic analyses for largemouth bass could serve as a model for the identification and evaluation of populations of fishes of many species and, thus, be effectively employed for fisheries management practices on a much broader scale. We feel this type of approach to fisheries management is imperative and that its implementation be immediate, for as Larkin (1978) stated, "... and looking ahead 75 years to the technologies that may be developed, it is abundantly evident that now is a good time for deciding on the objectives of fisheries management. If we wait much longer, many decisions will have been made by default, the consequences of which may be hard to undo."

Materials and Methods

Largemouth bass (20 individuals from each population sampled) were collected using a variety of techniques (electrofishing, seining, and rotenone sampling) by researchers

from a large number of different organizations. Fish were individually weighed, measured, wrapped in foil, and frozen to be shipped on dry ice and stored frozen until the electrophoretic analyses were performed. Tissue samples (white skeletal muscle, liver, and eye) were excised from frozen individuals and homogenized in two volumes of 100 mmol/L Tris−HCl, pH 7.0. This homogenate was centrifuged for 20 min at 20 000 × *g* at 4°C and the resulting supernatant was used for further analysis. The enzyme phenotypes encoded in each of 28 genetic loci were determined for each individual by vertical starch gel electrophoresis as described in Table 1. Histochemical staining was primarily based on the procedures of Shaw and Prasad (1970), but with modifications as described by Philipp et al. (1979).

TABLE 1. Electrophoretic procedures.

No.	Enzyme loci surveyed	Tissue analyzed	Electrophoretic[a] conditions	No. of alleles observed
1	*ADH-A*	Liver	HC	1
2	*GPDH-A*	Muscle	TC	1
3	*SDH-A*	Liver	HC	1
4	*LDH-A*	Eye	TC	2
5	*LDH-B*	Eye	TC	1
6	*LDH-C*	Eye	TC	2
7	*MDH-A*	Muscle	TC	3
8	*MDH-B*	Muscle	TC	2
9	*IDH-A*	Muscle	TC	1
10	*IDH-B*	Liver	TC	2
11	*6-PGDH-A*	Liver	HC	2
12	*GAPDH-A*	Muscle	HC	1
13	*GAPDH-C*	Eye	HC	1
14	*SOD-A*	Liver	TC	2
15	*AAT-A*	Muscle	TC	2
16	*AAT-B*	Liver	TC	4
17	*AAT-M*	Liver	TC	2
18	*CK-A*	Muscle	EBT	1
19	*CK-B*	Eye	EBT	2
20	*CK-C*	Eye	EBT	3
21	*AK-A*	Muscle	HC	1
22	*AK-B*	Eye	HC	2
23	*ALD-A*	Muscle	HC	1
24	*ALD-C*	Eye	HC	1
25	*PGM-A*	Muscle	TC	3
26	*GPI-A*	Eye	EBT	2
27	*GPI-B*	Muscle	EBT	2
28	*CBP-A*	Muscle	EBT	1

[a]HC: gel = 17.4% starch (w/v), 0.00125 mol/L histidine−NaOH, pH 8.4; electrode chambers = 0.10 mol/L citrate, pH 8.2; electrophoresis = 4 h at 225 V, 4°C. EBT: gel = 15.1% starch (w/v), 0.042 mol/L Tris, 0.023 mol/L borate, 0.00089 mol/L EDTA, pH 8.6; electrode chambers = (top) 0.18 mol/L Tris, 0.100 mol/L borate, 0.0036 mol/L EDTA, pH 8.6 and (bottom) 0.129 mol/L Tris, 0.07 mol/L borate, 0.0026 mol/L EDTA, pH 8.6; electrophoresis = 17 h at 225 V, 4°C. TC: gel = 18.6% starch (w/v), 0.0175 mol/L Tris, 0.0058 mol/L citrate, pH 7.0; electrode chambers = 0.075 mol/L Tris, 0.025 mol/L citrate, pH 7.0; electrophoresis = 18 h at 225 V, 4°C.

Results

Largemouth bass populations were sampled from 90 locations throughout the United States. The gene products at each of 28 loci were visualized by specific histochemical staining after vertical starch gel electrophoresis (Table 1). The genetic and molecular bases for these enzyme and isozyme systems are discussed in Philipp et al. (1979). The results of the electrophoretic analyses and a detailed assessment of the ecological correlates are given in detail elsewhere (Philipp et al. 1981a, b). The present report, however, will review these data and place a special emphasis on the management implications of our findings.

Of the 28 loci analyzed, 17 were found to be polymorphic (at a frequency of 0.025 or more) for at least 1 of the 90 populations studied (Table 1). At seven of the polymorphic loci (*GPDH-A*, *LDH-A*, *LDH-C*, *6-PGDH-A*, *CK-B*, *PGM-A*, *GPI-A*) variant alleles are rare and were observed in only one or a few individuals. The remaining 10 polymorphic loci exhibit allelic variation at a frequency greater than 0.05 in at least several populations. Of these 10 loci, 4 (*CK-C*, *AK-B*, *GPI-A*, *GPI-B*) reveal no obvious geographic patterns in the distribution of the alleles among the populations studied. An example of this apparently random distribution of two different alleles is observed at the *GPI-B* locus (Fig. 1). This pattern of allele distribution is not what one would expect if individuals, as a result of carrying these different alleles, were exhibiting different degrees of fitness for the different thermal environments.

The six remaining polymorphic loci (*MDH-A*, *MDH-B*, *IDH-B*, *SOD-A*, *AAT-A*, *AAT-B*), however, show nonrandom geographic distributions of alleles. The distributions of the alleles at these loci demonstrate that populations of largemouth bass from various regions of the country are genetically distinct. Genetic differences among largemouth bass have been inferred since the description of two distinct subspecies, the northern largemouth bass, *M. s. salmoides*, and the Florida largemouth bass, *M. s. floridanus* (Bailey and Hubbs 1949). The differences in their morphological characters suggested genetic differences. However, these characters cannot serve to quantitate the relative genetic contributions of the two subspecies to a mixed population of largemouth bass (Philipp et al. 1981a, unpublished results). In contrast, utilizing electrophoretic procedures, these relative genetic contributions can be quantitated, as the two subspecies of largemouth bass are fixed for a different set of alleles at two separate loci (Philipp et al. 1981a). Northern largemouth bass are fixed for the *IDH-B*^{1} allele, whereas the Florida largemouth bass are fixed for the *IDH-B*^{3} allele. (*IDH-B* is the isocitrate dehydrogenase locus, which in largemouth bass is expressed predominantly in the liver.) Intergrade populations contain both alleles. The geographic distribution of the *IDH-B* alleles among the largemouth bass populations studied is shown in Fig. 2. Similarly, northern largemouth bass contain *AAT-B*^{1} or *AAT-B*^{2} alleles, whereas Florida largemouth bass contain *AAT-B*^{3} or *AAT-B*^{4} alleles. (*AAT-B* is the aspartate aminotransferase locus, which in largemouth bass is expressed predominantly in the liver.) Intergrade populations contain up to four *AAT-B* alleles.

Bailey and Hubbs (1949) described the range of the apparently pure Florida largemouth bass as extending down peninsular Florida, south and east of the Suwannee River. Our electrophoretic analyses and morphometric measurements confirm this distribution (Philipp et al. 1981a, unpublished results). Furthermore, Bailey and Hubbs (1949) described the

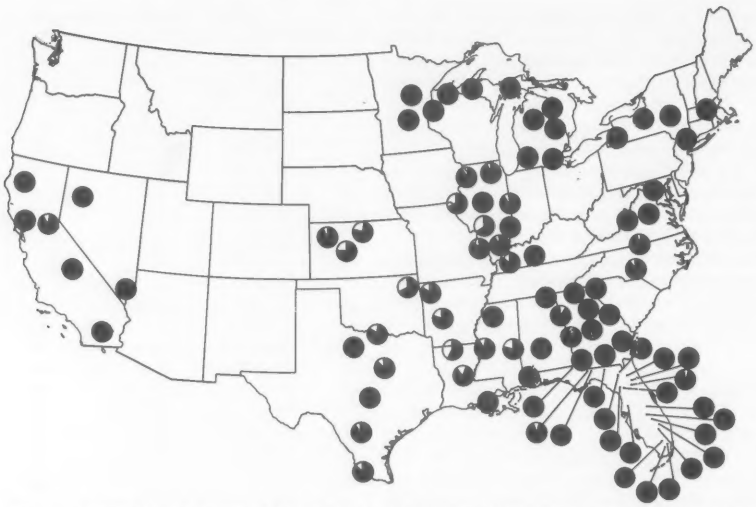

FIG. 1. Geographic distribution of the alleles at the *GPI-B* locus of largemouth bass. Black areas of the circles represent frequency of the B^1 allele, white areas the frequency of the B^2 allele, and spotted area the frequency of the B^3 allele.

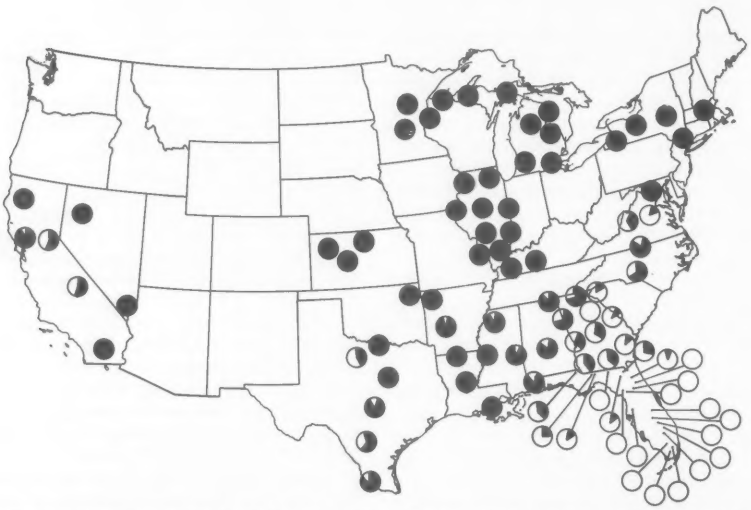

FIG. 2. Geographic distribution of the alleles at the *IDH-B* locus of largemouth bass. Black areas of the circle represent frequency of the B^1 allele and white areas the frequency of the B^3 allele.

range of the intergrade zone as consisting of northern Florida and most of Georgia, extending just over the borders of Alabama and South Carolina. However, our results clearly indicate that the existing intergrade zone extends considerably further than that previously postulated (Bailey and Hubbs 1949) to include Mississippi and the east coast north to Maryland (see Fig. 2 and Philipp et al. 1981a). Supplemental stocking efforts have clearly been responsible for the presence of the Florida largemouth bass in Texas and California. The reasons for the differences between the range of the intergrade zone determined electrophoretically (Philipp et al. 1981a) and that determined morphometrically (Bailey and Hubbs 1949) are not completely clear. For an extensive discussion of this issue see Philipp et al. (1981a). In any case, we have shown that the allele frequencies at two loci, *IDH-B* and *AAT-B*, can be used to estimate the relative contribution of the genomes of

FIG. 3. Geographic distribution of the alleles at the *MDH-B* locus of largemouth bass. Black areas of the circles represent frequency of the B^1 allele and white areas the frequency of the B^2 allele.

each subspecies within any largemouth bass population. The frequencies of the alleles at both of these loci describe a distinct latitudinal cline, with one allele (or pair of alleles in the case of *AAT-B*) having a frequency of 1.00 in the south but gradually decreasing to a frequency of 0.00 in the north. Similarly, latitudinal clinal distributions are apparent for the alleles at two other loci, *SOD-A* and *MDH-B*. (*SOD-A* is the superoxide dismutase locus, which in largemouth bass is expressed predominantly in the liver, whereas *MDH-B* is the malate dehydrogenase locus, which in largemouth bass is expressed predominantly in the white skeletal muscle.) Two alleles exist at the *SOD-A* locus. Northern largemouth bass are fixed for the *SOD-*A^2 allele. Florida largemouth bass contain this allele, as well as the A^1 allele. As a result, populations of largemouth bass in the southeast show a latitudinal cline in the distribution of these two alleles. A somewhat different situation exists at the *MDH-B* locus. Populations in the south, including all of those which consist of the pure Florida subspecies exclusively, are fixed for the *MDH-*B^2 allele (Fig. 3). However, the frequency of this allele decreased to 0.00 in some populations in the extreme northern parts of the range. The latitudinal midpoint of the clines at these four loci, *IDH-B*, *AAT-B*, *SOD-A*, and *MDH-B*, are different, suggesting that selective pressures acting on these different loci may be of different kinds or may be exerting their effects with different intensities.

Single variant alleles at each of two loci, *MDH-A* and *AAT-A*, show a fairly restricted geographic distribution, although no apparent clines are formed. (*MDH-A* is the malate dehydrogenase locus, which in largemouth bass is broadly expressed in most, if not all, tissues, whereas *AAT-A* is the aspartate aminotransferase locus, which in largemouth bass is expressed predominantly in the white skeletal muscle.) Most populations of largemouth bass are fixed for the *MDH-*A^1 allele. Populations along the extreme east coast, however, have significant numbers of a *MDH-*A^2 allele, indicating some degree of genetic distinctness for these populations. Similarly, most populations of largemouth bass are fixed for the *AAT-*A^1 allele, whereas certain populations in peninsular Florida contain a variant *AAT-*A^2 allele.

In summary, the combinations of the various possible alleles at each of these loci serve as genetic markers which indicate that populations of largemouth bass from different geographic regions are genetically distinct from one another. It is not unreasonable to propose that this genetic distinctiveness probably reflects the adaption of different populations to the environments of different geographic regions. Furthermore, the existence of the latitudinal clines in allele frequencies suggests that the thermal regimes of these different environments are acting as a potent selective force.

Discussion

The results of our electrophoretic analyses have revealed that largemouth bass from different regions of the country are genetically distinct. This difference is particularly pronounced for the two recognized subspecies, *M. s. salmoides* and *M. s. floridanus*, but pertains to populations within each subspecies as well. When the 90 populations studied in this report are grouped as to Florida subspecific, northern subspecific, and intergrade groups and compared, several facts become apparent. First, the average, unbiased genetic identity (Nei 1978) value (Table 2) for the 14 pure Florida largemouth bass populations (0.997) is greater than that for 31 pure northern largemouth bass populations (0.991) and still greater than that for the 37 intergrade populations (0.972). The intergrade populations exhibit the greatest degree of heterogeneity among populations within a group. When the pure subspecies

TABLE 2. Matrix of unbiased genetic identity coefficients (Nei 1978) averaged by subspecies.

Subspecies	No. of populations	Genetic identity I		
		1	2	3
1) Florida	14	0.997 (0.983–1.000)		
2) Northern	39	0.911 (0.879–0.940)	0.991 (0.955–1.000)	
3) Intergrade	37	0.960 (0.911–1.000)	0.962 (0.874–1.000)	0.972 (0.885–1.000)

are compared with the intergrades, the intergrade populations are nearly equivalently related to both subspecies. The average genetic identity value of 0.911 between the two subspecies provides fairly persuasive evidence of their genetic distinctness.

Most bodies of water in the United States that could possibly support a largemouth bass population have been stocked at least once and in some cases many times. The largemouth bass used to stock these waters have often been transported great distances and would be expected to have had quite different genetic backgrounds from those of the native populations. In view of the widespread occurrence of such promiscuous stocking, it is impressive that such distinct latitudinal clines in allele frequencies at several loci still exist. The persistence of these clines strongly suggests that powerful selective pressures are being exerted against many individuals that are inappropriately being introduced into these largemouth bass populations. Thus, stocking programs that involve introducing largemouth bass with a less than optimal genetic composition for a specific environment appear to be less than optimally efficient and effective. This would result not only in a waste of an important natural resource, but also in a considerable economic waste as well.

Physiological and morphological differences between the northern and Florida subspecies of largemouth bass have been well documented (Bailey and Hubbs 1949; Clugston 1964; Addison and Spencer 1972; Chew 1975; Crumpton and Smith 1975; Inman et al. 1976; Zolczynski and Davies 1976; Latta 1977; Botroff and Lembeck 1978; Moyle and Holzhauser 1978; Cichra et al. 1981; Wright and Wigtil 1981), although in most cases genetic confirmation of the subspecific purity of the stocks was not obtained. Although the thermal requirements of the two subspecies appear quite different, no quantitative data on this subject are available. We are currently trying to determine for each subspecies, as well as both reciprocal F_1 hybrids, such parameters as critical thermal maxima and minima, preferred temperature ranges, alpha-threshold temperatures of development, and the numbers of developmental thermal units required to reach hatching (Childers 1967). The different responses to these various thermal conditions and, hence, the different thermal requirements of the two subspecies are most likely under significant genetic control (Philipp et al. 1981b). The allelic differences in key metabolic enzymes encoded in certain loci (e.g. *MDH-B, AAT-B, IDH-B, SOD-A*) at least serve as genetic markers of physiologically different stocks and may well serve as a molecular basis for some of the thermal characteristics of these stocks.

Leigh-Brown (1977) outlines some of the criteria needed to assign a physiological difference to an allelic variation at a specific locus. First, the frequency of the alleles in the wild must vary significantly and correspond with the environmental factor responsible for the alleged selective pressure. An ecological basis for clines of total heterozygosity at enzyme loci has been proposed for some land vertebrates (Selander et al. 1971). Distinct latitudinal clines in allele frequencies have been observed in several fish species and have been attributed to the differential environmental temperatures found in various geographic regions (Koehn and Rasmussen 1967; Koehn 1970; Koehn et al. 1971; Nyman and Shaw 1971; Merritt 1972; Frydenberg et al. 1973; Johnson 1974; Avise and Smith 1974; Hjorth and Simonsen 1975; Nevo and Bar 1976; Johnson 1977; Borowsky 1977; Powers and Place 1978; Place and Powers 1979). Clines can also be generated by nonselective gene flow between populations which had been originally separated and had accumulated mutations differentially, but had subsequently been reconnected (Kimura and Ohta 1971; Ohta and Kimura 1971; Aspinwall 1974). Another criterion to be met is that individuals with one phenotype be affected differently by the purported selective force compared with individuals of the other phenotype. The differential action of a selective force upon individuals of differing phenotypes has been shown to exist for several organisms (Johnson 1971; Yardley et al. 1974; Avise and Smith 1974; Nyman 1975; Mitton and Koehn 1975; Nevo et al. 1977). The last major requirement to be met is that the allelic isozymes encoded at the suspected locus should behave differently in vitro when exposed to different conditions mimicking the proposed selective force. This has been demonstrated for several cases (Koehn 1969, 1970; Merritt 1972; Place and Powers 1978; Richmond and Zimmerman 1979).

Based upon the existence of such distinct latitudinal clines in allele frequencies, we believe the allelic differences at one or several loci (e.g. *MDH-B, IDH-B, SOD-A, AAT-B*) may serve to determine the thermal characteristics of largemouth bass. We have met several of the above criteria for demonstrating selection and have established the existence of clines of allele frequencies (Philipp et al. 1981a, b). We have detected kinetic differences between the *MDH-B* allozymes (Hines et al. 1981). However, similar experiments should be carried out with the allelic isozymes encoded at the other loci, as well. Childers (1979) showed that northern largemouth bass in Sangchris Lake, Illinois, with different *MDH-B* phenotypes reacted differently to thermal stress imposed upon them by thermal effluent from a coal-fired electricity generating power plant. As a result, the physiological and genetic differences seen among largemouth bass seem closely interrelated and serve to define quite different stocks. These different stocks

should be individually managed and utilized to obtain maximum benefits.

It is imperative that hatcheries utilize brood stock with genetic compositions appropriate for the geographic locations they serve. A large facility serving a wide geographic area may need several different brood stocks which would be genetically distinct and designed to produce distinct stocks of bass suited for distinct environments. This type of facility would be particularly important for states in which different environmental conditions exist in one area compared with another. Such a facility would also be important for those states in the intergrade zone between the two subspecies. For example, bass to be produced for stocking in southern Alabama or Georgia should have considerably higher frequencies of the *MDH-B*^{2}, *IDH-B*^{2}, *AAT-B*^{3} or *B*^{4}, and *SOD-A*^{1} alleles than bass to be produced for stocking in the northern areas of these states.

In addition, certain states outside of the natural intergrade zone are currently stocking "Florida bass" in a number of different programs (Sasaki 1961; Botroff and Lembeck 1978; Moyle and Holzhauser 1978). To evaluate accurately the success of these programs, the genetic composition of the Florida brood stock should be confirmed and should be stringently protected against contamination with northern subspecies brood stock and vice versa. Unknowing contamination would allow for the indiscriminant and, quite probably, unwanted transportation of some Florida alleles to lakes in which the existing bass population could very well be adversely affected. Furthermore, such monitoring of the genetic structure of bass populations would prevent the inadvertent contravention of certain states' fishery statutes, such as Illinois, in which importation of the Florida subspecies is currently restricted.

For these reasons, it is imperative that each state and federal fish hatchery define the various geographic regions it will serve and then analyze the genetic composition of the largemouth bass being produced. If the stock was found to be unfit for the geographic area being served by the hatchery, new brood stock should be selected which would produce largemouth bass better suited for stocking lakes in these areas. A national program should be initiated to evaluate hatcheries across the country. Hatcheries could then alter or add to their brood stocks to insure production of appropriate largemouth bass, which may mean constructing several distinct stocks to be used for various geographic areas. It must be stressed, however, that this does not represent an endorsement of the production of inbred lines. The high levels of genetic variability inherent in any natural population must be protected during the production of any group of hatchery fry. This is essential for maintaining vigorous, productive stocks and may require the routine replacement of brood parents with wild individuals of appropriate genotypes. The Illinois Department of Conservation, in conjunction with the Illinois Natural History Survey, is currently conducting such a program. A highly integrated program of this type designed to meet the nation's supply and demand of largemouth bass for all geographic areas would require a certain amount of effort initially, but more efficient utilization of the largemouth bass produced would, in the long run, result in an overall savings of natural and human resources.

As fish populations have been genetically tailored for their specific environments through long-term natural selection, an alteration in the environment could result in a population instantly becoming less than optimally fit. Major environmental alterations could result in quite catastrophic alterations in an existing largemouth bass population. For instance, the addition of heated effluent to a lake could possibly alter the annual thermal regime of that lake to such an extent that the new thermal environment is much closer to one located hundreds of miles to the south (Coutant 1975a, b). Thus, a different genetic stock of largemouth bass may better suit the new thermal regime. This situation could be anticipated and the adverse effects reduced by corrective stocking procedures in which largemouth bass of more southern phenotypes would be supplementally stocked. The overall goal would be to have a largemouth bass population that maximally utilized the existing thermal regime of that lake. Unfortunately, thermal alterations of this type have additional problems. For instance, often the entire lake is not uniformly altered. Some portions of a given cooling lake may actually experience very little thermal alteration (Larimore and Tranquilli 1980). Another particularly difficult problem arises when there are sudden perturbations in temperature, as when the heated effluent ceases in midwinter and ambient temperature drops extremely rapidly to levels definitely stressful to the existing largemouth bass which have been genetically tailored and thermally acclimatized to the warm environment. Situations like these, in which the thermal environment is quite heterogeneous spatially or temporally, would then require populations of bass that would be highly flexible in their thermal responses. In the future it may be possible to identify or to construct a genetic stock in which the individuals are themselves physiologically flexible enough for these types of thermal environments, but for now, perhaps the best suited largemouth bass population would be one with a maximal amount of genetic variation, so that an entire range of phenotypic combinations and, hence, thermal responses would be present.

In summary, we have shown that genetic differences exist among largemouth bass populations throughout the United States. These genetic differences have resulted from long-term exposure to natural selective pressures and provide the species with enough variation to deal with the large range of different environmental conditions in which it exists. Fisheries biologists could use these genetic data to construct specific strains of largemouth bass for specific environments. This would not only help to maximize efficiency in the use of human resources in fisheries management, but also help to maximize utilization of the environmental resources by the largemouth bass. This combination would help create the highest quality largemouth bass fishery.

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Native Lake Trout (*Salvelinus namaycush*) Stocks in the Canadian Waters of Lake Superior Prior to 1955[1]

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GOODIER, J. L. 1981. Native lake trout (*Salvelinus namaycush*) stocks in the Canadian waters of Lake Superior prior to 1955. Can. J. Fish. Aquat. Sci. 38: 1724–1737.

The decline of Lake Superior lake trout (*Salvelinus namaycush*) stocks after the sea lamprey (*Petromyzon marinus*) population explosion of the 1950s was both dramatic and decisive. Few native stocks remain to permit scientific data collection. However, interviews with old-time commercial fishermen suggest that there had existed many discrete or semi-discrete stocks within the lake. Historical documents in the form of government correspondence and reports, explorers' accounts, and Hudson's Bay Fur Co. records yield further evidence.

Possible stocks are distinguished on the basis of anatomical features (including weight, body shape, and coloration) and behavioral differences (including seasonal movements and spawning habits). The relevance of these criteria for stock identification is discussed.

Fishermen distinguished four general categories of *S. namaycush*: leans, fats or siscowets, half-breeds, and humpers or paperbellies. In addition, different "breeds" or forms of lean trout were commonly recognized. Often a form was known by a name referring to its most distinctive feature: blacks, redfins, yellowfins, grays, salmon-trout, red trout, moss trout, sand trout, and racers. These varieties are discussed and local spawning habits, grounds, and movements are summarized with maps, tables, and text. At least 200 former spawning grounds are identified, including 20 rivers which were once characterized by September runs of lake trout. Spawning locations for the deep-water, nonlean trout variants (paperbellies, half-breeds, and siscowets) are less easily discovered. Approximately 35 fishing grounds are noted, with spawning reported at 4 of these. Consideration is given to the possible existence of phenotypically distinct stocks of siscowet.

Key words: lake trout, *Salvelinus namaycush*; stocks, anatomical features, behavioral differences

GOODIER, J. L. 1981. Native lake trout (*Salvelinus namaycush*) stocks in the Canadian waters of Lake Superior prior to 1955. Can. J. Fish. Aquat. Sci. 38: 1724–1737.

Le déclin des stocks de touladis (*Salvelinus namaycush*) du lac Supérieur après l'explosion de la population de grandes lamproies marines (*Petromyzon marinus*) des années 1950 fut à la fois dramatique et décisif. Il reste peu de stocks indigènes sur lesquels prélever des données scientifiques. Cependant, si l'on en croit les anciens pêcheurs, il y avait dans le lac plusieurs stocks distincts ou semi-distincts. Ceci est appuyé par des documents historiques, tels que correspondance et rapports gouvernementaux, comptes rendus d'explorateurs et dossiers de la Compagnie de la baie d'Hudson.

On peut différencier des stocks possibles par certaines caractéristiques anatomiques (y compris poids, forme du corps et coloration) et par des particularités du comportement (y compris déplacements saisonniers et moeurs reproductrices). Nous examinons la pertinence de ces critères dans l'identification des stocks.

Les pêcheurs distinguaient quatre catégories générales de *S. namaycush* : maigres, gras ou siscowets, métis et bossus ou « paperbellies ». Ils reconnaissaient en outre différentes « races » ou formes de touladis maigres. On désignait souvent une forme par sa caractéristique la plus distinctive : noirs, nageoires rouges, nageoires jaunes, gris, truites saumonés, truites rouges, truites de mousse, truites de sable et coureurs. Nous examinons ces variétés et résumons, à l'aide de cartes, tableaux et texte, les moeurs reproductrices locales, les frayères et les

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déplacements. On a pu identifier au moins 200 anciennes frayères, y compris 20 rivières jadis caractérisées par des remontées de septembre des touladis. Il est plus difficile de découvrir les frayères des variants d'eau profonde de touladis non maigres (« paperbellies », métis et siscowets). Nous mentionnons environ 35 lieux de pêche, à 4 desquels la ponte a été signalée. Nous examinons la possibilité de l'existence de stocks de siscowets phénotypiquement distincts.

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COGNIZANT of the severe losses inflicted on Lake Superior lake trout (*Salvelinus namaycush*) by the sea lamprey (*Petromyzon marinus*), both Ontario and American state governments embarked upon extensive restocking programs. Despite concerted efforts at rehabilitation, however, viable, self-reproducing populations have failed to re-establish themselves in large areas of the lake; here the catches are still predominantly of hatchery-reared lake trout. It is the opinion of some biologists that this slow rate of success has been due, in part, to early failures at tailoring planting strategies to the different site requirements and ecological characteristics of the lake's various trout stocks.

Although fisheries biologists are now aware that effective management must consider species on the level of individual stocks, only limited attempts have hitherto been made to identify lake trout stocks within the Great Lakes (Van Oosten 1927; Smith 1968; Organ et al. 1978; Peck 1978).

This paper provides historical background information by delineating traditional Canadian Lake Superior spawning grounds and identifying possible stocks existing prior to the advent of *P. marinus*. A study such as this is particularly relevant to Lake Superior for a number of reasons: (1) It is the largest of the Great Lakes and supported an important lake trout fishery. (2) Destruction of the native stocks has occurred more recently than in the other Great Lakes; therefore, proportionately more people are still alive who were familiar with these stocks. (3) As stated above, government agencies have placed special emphasis on trout rehabilitation for the lake. (4) Of all the Great Lakes, lake trout stock formation seems to have attained its greatest diversity in Lake Superior.

Fishermen have traditionally distinguished four general categories of lake trout within Lake Superior waters: leans, paperbellies or humpers, half-breeds, and fats or siscowets. Each tended to dictate different techniques for fishing and brought different prices at market (Lawrie and Rahrer 1973). Recent studies have allotted the first and the last subspecific status (Thurston 1962; Eschmeyer and Phillips 1965; Khan and Qadri 1970).

Within the category "lean lake trout," fishermen also claim the former existence of specific forms or "breeds," based on observed differences in behavior, habitat, and physical appearance. These differences became most apparent during the spawning season. A particular form may have been quite site specific, spawning only on certain selected grounds. On the other hand, a form may have constituted a general spawning run of fish, appearing at many places along the shores or shoals. (In illustration, Table 1 summarizes two historical descriptions of lake trout forms: the first pertains to the Upper Great Lakes in general, whereas the second refers strictly to the St. Ignace Island area of northern Lake Superior.)

The forms of lake trout described by fishermen imply, in certain instances, some degree of intraspecific isolation and stock formation. Historical documents suggest that people have recognized such stocks for many years; although incorrect in their penchant for assuming new species or subspecies, their observations were not without biological significance. Today there remain but scattered remnants of these original stocks.

Sources of Information

During the summers of 1978 to 1980 I interviewed ~85 commercial fishermen, sportsmen, and charterboat operators who had been personally involved with the pre-1955

TABLE 1. Historical examples of Great Lakes lake trout variants.

A) Goode (1884)
(In the summer of 1880 Louis Kumlien investigated the subject of local varieties of lake trout)
1) Green Bay Vicinity
Black Trout — salmon-colored flesh
Lake Trout — white flesh
2) Eastern shore of Green Bay, on the eastern shore of Lake Michigan
Two species of Mackinaw trout recognized by fishermen
3) Grand Traverse Bay, Lake Michigan
Reef trout — long, slim, coarse-meated variety taken in shallow water: when large called racers
Potbellies — short chubby variety, taken in deep water
4) Vicinity of Two Rivers, Wisconsin
Reef trout — large, lank, coarse flesh (see above)
Other form more highly prized, taken in deep water
5) South end Lake Michigan
Two forms, one darker-colored with red flesh being the more highly prized
6) Grand Haven
Two forms of Mackinaw Trout — Shoal-water trout and Deep-water trout
7) Thunder Bay, L. Huron vicinity
"Buckskin" — held in high esteem
Racer

B) Thomson (1883)
Varieties of trout
1) Salmon trout, weight up to 70 lb (1 lb = 0.454 kg)
2) "Siskowitt," weight up to 12 lb
3) Half-breed siskowitt, weight up to 5 lb
4) "Potgut," very inferior fish, weight up to 12 lb
5) Rock or black trout, weight up to 40 lb
6) Large gray or shovel-nose trout, weight up to 70 lb
7) "California trout," yellow spots and flesh, weight up to 10 lb
8) "Half-breed red trout," weight up to 15 lb
9) Common brook or speckled trout, weight up to 7 lb
10) Red trout, weight up to 42 lb

Canadian lake trout fisheries. It became evident that small-boat fishermen sometimes formed impressions of fish habits and habitats different from those of the large-scale tug operators, who could roam farther afield but tended to know individual grounds less intimately. The western end of the lake, with its greater number of sheltered bays, island areas, and nearshore grounds, has traditionally been more accessible to the former. Therefore, all efforts were made to corroborate verbal evidence, and this was possible for most areas of the lake. It should be noted, however, that certain regrettable gaps exist in the spawning ground maps, notably between Pukaskwa and Pic rivers, and along the north part of the Black Bay Peninsula. These are lonely stretches of shore, distant from fishing ports.

Fishermen were requested to indicate on Canadian Hydrographic Service (or National Oceanic and Atmospheric Administration) Great Lakes navigation charts the native lake trout spawning grounds with which they were familiar. These grounds, with the forms (or runs) of lake trout reported as having been dominant, are summarized in Fig. 1–3. Lake trout names are those employed by the interviewees. Spawning periods are reviewed in Table 2 and possible stocks noted.

Archival records were also consulted, and included many published and unpublished accounts of explorers, settlers, sportsmen, and naturalists. Especially useful were the journals and reports of the 19th century Hudson's Bay Company Posts on Lake Superior, and the overseers' reports and correspondence retained in the holdings of the federal Department of Fisheries and Oceans (in the Public Archives of Canada, Ottawa).

Criteria for Stock Identification

Fishermen tended to distinguish groups of lake trout on the basis of the following criteria.

Spawning Location and Time

Throughout the early years of Canadian fisheries management, much heated debate centered on whether closed season regulations were representative of the true spawning periods of the fish species they were designed to protect. It became obvious that the gravidity of a particular species could vary widely under the influence of genetic makeup, age, and local conditions such as food supply, current, and temperature. In bodies of water as vast as the Great Lakes, even the whole lake could not be considered as a single spawning unit. Along certain stretches of Great Lakes shoreline serial trends in annual lake trout spawning periods have long been recognized (see, for example, Smith 1968). In eastern Lake Superior, for instance, the commencement of spawning became progressively later from north to south. It was the practice of some fishermen to begin their fall season at the Pukaskwa River, moving to the Eagle River, the Dog (and sometimes the Bear) River, and lastly the Montreal River in order to sequentially exploit different shore- and river-runs. A similar latitudinal trend was evident along the Black Bay Peninsula: spawning at its northern end began 1 wk to 10 d earlier than at Thunder Cape.

Local conditions might obscure such general trends. Different groups of lake trout seemed to show temporal or habitat segregation according to whether they spawned in river, shore, or shoal areas, windward or leeward zones, bay or mainshore areas, and deep or shallow waters. Lake Superior river-running stocks, for example, often spawned somewhat earlier than those along adjacent main shores. Stocks frequenting the warmer waters of a bay (such as Nipigon Bay) might ripen more slowly and so be reproductively isolated from those of the main lake.

The earlier reports of intraspecific differentiation among Great Lakes *S. namaycush* date from the 17th century and the Jesuit Relations (1670–71). Later historical documents pertaining to the Upper Great Lakes fisheries often noted two visibly distinct runs of lake trout: one spawning inshore and another frequenting offshore shoals (United States House of Representatives 1897; Cook 1929). The spawning scenario of Lake Superior could be considerably complicated, however, by the multiple use of grounds by more than one apparently distinct breeding group. In certain areas this resulted in a rather extended spawning period (as was the case among the islands south of Nipigon Bay). Successive runs showed definite peak concentrations of individuals separated in time by up to 2 wk or more. Despite some intermingling of different runs, patterns seem to have remained consistent through many years. In addition, the close proximity of certain breeding grounds, characterized by different spawning periods, suggests the sympatric association of different groups of trout varying in their responses to spawning stimuli.

Body Weight and Form

As a general rule, seasonally later runs were composed of larger and heavier fish. Several factors might account for these interrun size variations: (1) differences in age composition (perhaps younger fish spawned earlier); (2) differences in growth rates (perhaps the early spawners had slower growth rates or more precocious maturation rates); (3) differences in percentage sex composition; (4) the occurrence of fishing-up phenomena, whereby large individuals were selectively cropped from more heavily exploited fish groups. Obviously these factors can be interrelated, and growth and maturation rates may be influenced by a variety of environmental factors, including water temperature, diet, and fishing pressure. Nevertheless, consistencies were found in the modal weights fishermen reported for each run. It seems that there were not merely intergradations of sizes arriving on the grounds, but actual pulses of different size-classes, an annual stability in composition which may, in some cases, have been linked to local racial differences, (Weight summaries are provided in Table 3.)

Reported variations in body form between lake trout of different grounds, or between different runs on the same grounds, are discussed in later sections. Variations in body form between segments of a population can relate to different rates of growth (Martin 1949).

Flesh Coloration

Although the role of carotenoids in coloring Salmoninae flesh has been known for years (Stevens 1948; Goodwin 1954), the relative importance of various factors determining the intensity of coloration remains in question. Whereas some

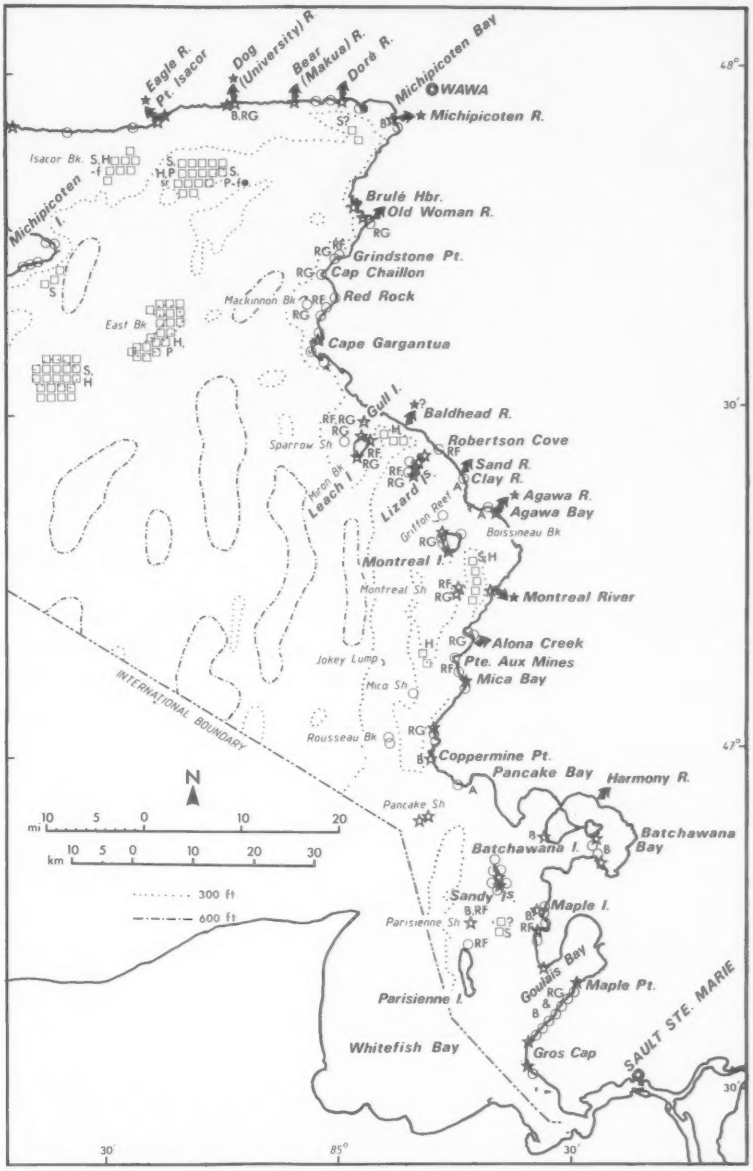

FIG. 1. Sault Ste. Marie to Michipicoten Island. Fishing grounds (nonlean fish only) and spawning grounds of native lake trout. Varieties of native lake trout (names are those employed by fishermen). Leans: RG, regular; B, black; RF, redfin; RD, red; Y, yellowfin; G, grey; ST, Salmon-trout; A, Sand trout. Spawning grounds for lean lake trout. Shore or shoal: ☆, major; ○, average (or of unknown importance); ms, "moss" areas (see text). Rivers: ★, major; ◓, minor (or of unknown importance). Nonleans: S, siscowet (or fat); H, half-breed; P, paperbelly (or humper); □, fishing grounds for nonlean lake trout; ●, spawning reported for nonleans. Spawning location or variety uncertain indicated by question mark (?). Fishing season: sp, spring (April–June); sr, summer (July–Aug.); f, fall (Sept.–Nov.). Fishing gear: gn, gill nets; tr, trolling; pn, pound nets.

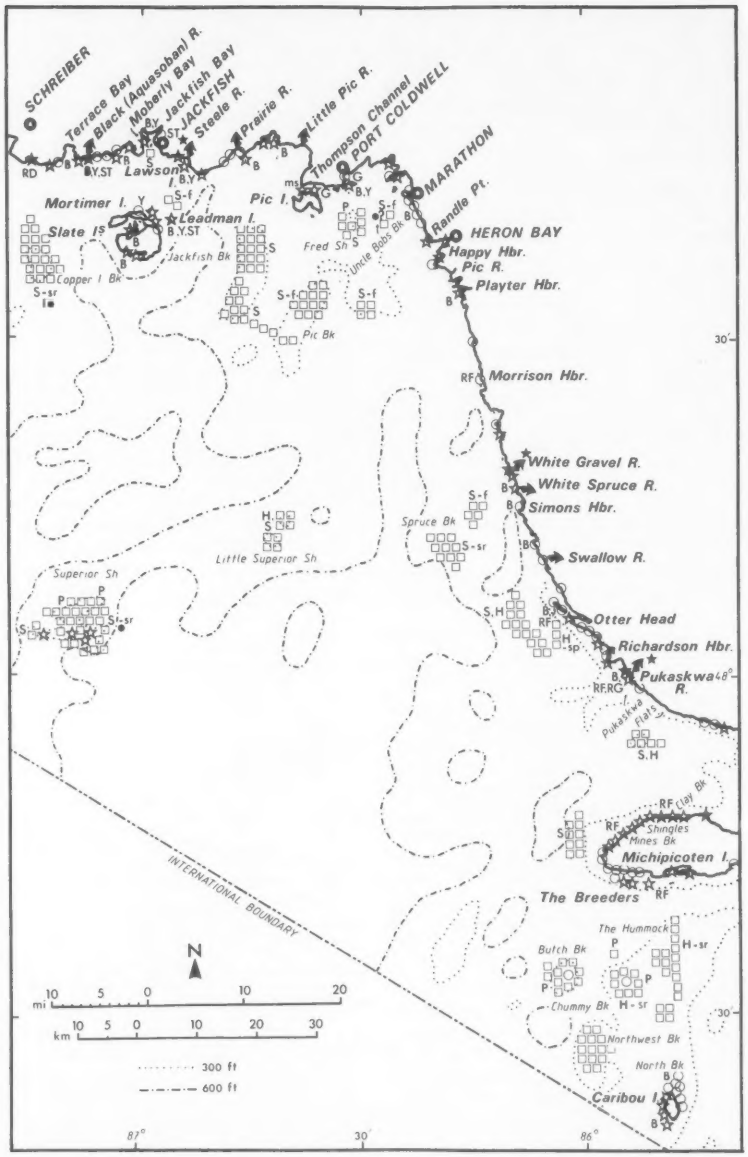

FIG. 2. Michipicoten Island to Schreiber. For explanation of abbreviations, see legend to Fig. 1.

researchers have stressed genetic controls (Prince 1916), others have outlined the significance of environmental determinants such as diet (Hacker 1962; Peterson et al. 1966), age and size (Nilsson and Andersson 1967), or sexual condition (Miller and Kennedy 1948; Rawson 1961). Thus one might regard flesh coloration as an unreliable stock indicator due to the interaction of environmental and physiological factors in masking its genotypic expression. In Lake Superior, however, visible flesh differences existed between the trout of certain spawning runs and/or shoals and remained consistent from year to year. The persistence of different flesh forms may relate to the operation of mechanisms ecologically

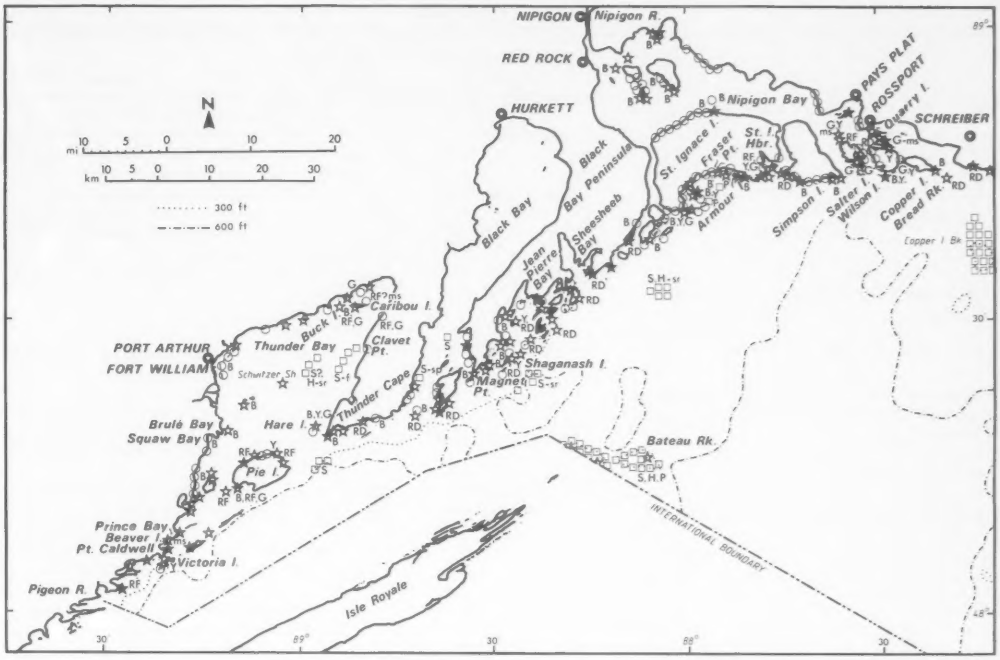

FIG. 3. Schreiber to Pigeon River. For explanation of abbreviations, see legend to Fig. 1.

TABLE 2. Spawning grounds and periods for Lake Superior lean lake trout. For explanation of abbreviations, see legend to Fig. 1.

Location	Approx. spawning period: Start	Approx. spawning period: Finish	Dominat variety	Comment
		A) Shore, shoal, and bank areas		
Sault Ste. Marie to Michipicoten Island (Fig. 1)				
Gros Cap to Maple Point	1st wk Oct.		B, RG	
Maple Island	Oct. 5–10	For 7–10 d	B	Spawning heavier than along main shore
	Oct. 15	End of Oct	RF	2 distinct runs
Parisienne shoal	Oct. 15–20	For 7–10 d	B	Offshore stocks, spawning later than those near shore
			RF	2 distinct runs
East Batchawana Bay	Oct. 10		B	Small B, probably a discrete stock
Outside Batchawana Island	Oct. 10–15		B	
South Sandy Island	Oct. 15–20			
Pancake Bay Flats			A	Observed in summer and fall (see text)
Mica Bay, Pte. Aux Mines	Oct. 1	Oct. 15 (?)	RF	Run unique to this area
Montreal Shoal	Sept. 28–Oct. 1	Early Oct.	RG	Possible stock of large RF
	Oct. 10–25	Nov. or early Dec.	RF	
Montreal Island	Oct. 5–10	Oct. 25	RG	
Boissineau Bank			See comment	Unique form to this area (deeper body, thinner ventral region, color differences from other leans) taken in late summer
				Spawning location unknown
Agawa Bay	Late Sept.		RG, A	
Clay River and Sand River area			A	
Lizard Island	Oct. 5–10	Oct. 25 or later	RG, RF	
Robertson Cove			RF	Possible stock
Leach Island	Oct. 5–10	Oct. 25 (?)		

TABLE 2. (*Continued*)

Location	Approx. spawning period		Dominant variety	Comment
	Start	Finish		
Sparrow Shoal	Oct. 5–10	Oct. 25	RG	Especially large trout
Gull Island	Oct. 10–25	1st wk Nov.	RG, RF, see comment	In addition to RG and RF, form having unique skin coloration (silver–green body with large darker spots)
Mackinnon Bank	Oct. 15	Up to 1st wk Nov.	RF	Possible offshore spawning stock
Red Rock	1st wk Oct.		RG, see comment	In addition to RG, spawning form known as "half-dollar trout" (colored fins, pink flesh, coin-sized markings on silver–gray bodies)
North point of Old Woman Bay	Late Sept.		RG	
Brulé Harbor	3 days after Old Woman Bay		RG	
	Nov.		See comment	Large late spawners at 18 m (60 ft); deeper than RG
Michipicoten Bay	3rd wk Sept.		B, RG, RF	
Michipicoten Island to Schreiber (Fig. 2)				
Pukaskwa Flats	Early Sept.		B, RG, RF	
Richardson Harbor	Sept. 10			
Otter Head		After Oct. 15	B, RF	Possible stocks of B
Clay Banks, The Shingles, Mines Bank (Michipicoten Island)	Early Oct.	3rd wk Nov.	RF	Probable stocks of RF
Chummy, Northwest, The Hummock Banks				Stocks of leans Spawning habits not known
Butch Bank				Stock of leans smaller than those of the above banks
Caribou Island	Oct. 1	Oct. 22	B	Probable stock
Simons Harbor			B	Possible stock
White Gravel River area	Sept. 7		B	Stock of late-spawning RF?
	Nov. 1		RF	
Playter Harbor, Happy Harbor, Randle Point	After Sept. 7		B	
Port Coldwell area			Y, G (ST)?	Probable stocks
Thompson Channel	Nov.		G	Spawning in "moss" areas (see text)
Lawson Island	Sept.	Nov.	B, Y	
Leadman Island			B, Y, ST	Probable stocks Large trout more abundant than at Slate Islands
Slate Island	Sept. 20–25	For 2 wk (longer in sheltered areas)	B	Stocks probably discrete from those of mainland
North Mortimer Island (Slate Islands)			Y	
Jackfish Bay area	Sept. 20–25	For 10 d–2 wk	B	
Moberly Bay, Cody Island (Jackfish Bay)	Oct. 1 or later		Y	Possible stock Racer form also reported
East arm of Jackfish Bay			ST	Possible minor stock
Superior Shoal	July? Sept.?		See text	Discrete stocks, possibly associated with particular banks Numerous instances of deformity and cannibalism
Schreiber to Pigeon River (Fig. 3)				
Among islands south of Rossport and Nipigon Bay	Sept. 22	Oct. 10	B	
Bread Rock, Quarry Island	Oct. 5	Oct. 15	RD	Possible stocks? (see text)
Quarry Island, Rolette Shoal (North Salter Island)	Nov.	Dec.	Y, G	Spawning in "moss" areas (see text)
West Wilson Island, Salter Island, St. Ignace Harbor	Mid Nov.	Dec.	G	Probable stocks of late spawners
Nipigon Bay	Sept. 30		B, silver-colored trout	Probably discrete stocks

TABLE 2. (*Concluded*)

Location	Approx. spawning period		Dominant variety	Comment
	Start	Finish		
Armour Island, Fraser Point	Oct. 5	Oct. 15	RD	Possible stocks?
Sheesheeb Bay area	Sept. 17		B	
Sheesheeb Bay			See comment	Small trout in June distinct in appearance from those of main shore (stockier, coloration differences)
				Spawning habits not known
Shaganash Island	Sept. 20	Mid Oct.	B	Possible stock of Y
	Late Oct.		Y	
Magnet Point	Sept. 20		B	
Black Bay				Spawning stocks move only to south portion
Thunder Cape	Sept. 30		B	
Blateau Rock			See text	Probable discrete stocks of leans
Hare Island Reef	Sept. 30–early Oct.	Nov.	B, Y, G	
6.5 km (4 mi) north of Clavet Point		Nov.		Possible stock of late spawners
South shore of Caribou Island	1st wk Oct.		B	
	3rd wk Oct.		RF	
North shore Caribou Island			RF(?), G	Spawning in "moss" areas
North end Thunder Bay		Dec		Unusually late spawners
Buck Island			G (?)	Large, late spawners
Breakwall at Port Arthur and Fort William	Late Sept.–early Oct.		B	
Schwitzer Shoal				Probable stock
Grand Reef (Brulé Bay)	Sept. 25	Oct. 2	B	
South of Squaw Bay	Mid. Sept.		B, "little grays"	
Pie Island	Sept. 15	Late Sept.	B	
	Oct. 20		RF	
	After Oct. 20		Large RF	
Northwest shore Victoria Island	Nov.		Y	Probable stock
Beaver Island			G (?)	Spawning in "moss" areas"
Caldwell Shoal (Point Caldwell)	1st half Nov.		Large spawners	Possible stock
		B) Major spawning rivers		
Montreal River	Sept. 20–25	Oct. 10–15		
Michipicoten River	Sept. 17	Sept. 27–Oct. 8		
Dog River	Sept. 17	Sept. 30 (Loftus 1958)		
Eagle River	Before Dog River			
Pukaskwa River	Sept. 1–5	Late Sept.		
Steele River	Sept.			

separating groups of lake trout during some portion of their lives. For example, to the extent that flesh color is diet related, one might posit the existence of dissimilar feeding niches.

SKIN COLORATION

Agassiz (1850) noted several local color variants in Lake Superior lake trout and believed these to be dependent on habitat bottom. As discussed below, more recent fishermen also recognized an assortment of comparable color types. The frequent heterogeneity of type at a single spawning location suggests the influence of other factors in addition to local substrate. On the basis of behavioral and spawning patterns described by fishermen, it is probable that coloration represented the natural spawning period responses of certain groups of Lake Superior lake trout and could be used to distinguish them at this time. Precedents exist for the use of skin coloration as partial criterion for salmonid stock identification (Ricker 1959; Bulkley 1963; Nilsson and Filipsson 1971).

NONSPAWNING MOVEMENTS

Distinct groups of lake trout were less obvious at times other than the spawning season. However, fishermen frequently reported both vertical and horizontal segregation of large and small trout. Those caught in bottom nets set at 55 m (180 ft) to 75 m (245 ft) in the spring were usually of smaller size. As the weeks progressed many lake trout migrated into shallower zones along both offshore shoals and shore banks. In June or July larger (and older) fish tended to become

TABLE 3. Weight summaries of lake trout varieties reported by Lake Superior fishermen. For explanation of abbreviations, see legend to Fig. 1.

Location	Variety season, gear	Weight range (kg(lb)) Min.	Max.	Avg.
	Leans			
Sault Ste. Marie to Michipicoten Island (Fig. 1)				
East Batchewana Bay	B, f, gn			0.9(2)–1.4(3)
Pancake Point to Coppermine Point	B, f, gn	1.1(2.5)	2.7(6)	1.8(4)
Montreal Shoal	sr, tr		9(20)	1.4(3)–1.8(4)
Jokey Lump	sr, tr	3.6(8)	8(18)–11(24)	
Miron Bank	sr, tr	2.3(5)	25(55)	
Mackinnon Bank	sr, tr		14(30)	
Red Rock	"Half-dollar trout," f, gn			7(15)
(River spawners)				
Montreal River	f		9(20)–16(35)	3.6(8)–4.5(10)
Dog River	f		6.4(14)	1.8(4)–3.2(7)
Michipicoten Island to Schreiber (Fig. 2)				
Michipicoten Island	sr, tr		6.8(15)–14(30)	
Butch Bank	sr, f			0.68(1.5)–0.91(2)
Caribou Island	B, sr, f		4.5(10)	2.7(6)
Steel River mouth	sr, tr		14(30)	2.3(5)–4.5(10)
Jackfish Bay area	B, f, gn		3.6(8)	2.7(6)
Jackfish Bay area	Y, f, gn	5.4(12)	11(25)	
Jackfish area (main shore)	sp, gn			1.1(2.5)–1.4(3)
Slate Island (River spawners)	B, f, gn		2(4.5)	1.4(3)
Pukaskwa River	f	1.4(3)–1.8(4)	>8.2(18)	
Schreiber to Pigeon River (Fig. 3)				
Among islands south of Rossport and Nipigon Bay	B, f, gn		4.5(10)	1.4(3)–2.3(5)
	Y, f, gn	5.4(12)	9.1(20)–23(50)	
	July, pn		4.5(10)–6.4(14)	
Armour Island, Fraser Point	RD, f, gn		6.8(15)	
Nipigon Bay			2.3(5)	
Black Bay Peninsula	B, f, gn		3.2(7)	0.9(2)–2.3(5)
Sheesheeb Bay	June		2(4.5)	0.9(2)–1.4(3)
Jean Pierre Bay area	RD, f, gn	2.3(5)	6.8(15)	
Bateau Rock		1.1(2.5)	3.2(7)	
Hare Island	Y, f, gn		23(50)	
Buck Island	RF, G f, gn		24(54)	
Grand Reef (Brulé (Bay)	B, f, gn		3.6(8)	
South of Squaw Bay	"Little grays," f, gn			1.8(4)

TABLE 3. (*Concluded*)

Location	Variety season	Weight range (kg(lb)) Min.	Max.	Avg.
Pic Island	RF, f, gn		11.3(25)–13.6(30)	6.8(15)
	Nonleans			
Between Montreal Shoal and Montreal Island	H, gn	0.7(1.5)	2.7(6)	
	S, gn	2.7(6)	5.5(12)	
Port Coldwell vicinity	P, June, gn			1.8(4)–2.7(6)
Pic Bank	S, Aug., f, gn	4.5(10)	9.1(20) 11(25)	
Copper Island Bank	S, Aug., f, gn		11(25)	
(Historical references)				
Lake Superior (Herbert 1851)			7.7(17)	1.8(4)–2.3(5)
Lake Superior (Lanman 1847)			5.4(12)	
Lake Superior (Sweeny 1880)			14(30)–41(90)	

pelagic, at which time fishermen knew them to feed on cisco stocks or insects at the surface (see also Lawrie and Rahrer 1973). Nearshore movements might be referred to as "summer runs," which continued for several weeks in certain areas. Their availability was under the strong influence of wind and temperature. Dates for the commencement of movements to shallow waters also varied with location in any particular year. In Michipicoten Bay, for example, trout moved into shallow waters in late June, earlier than in the vicinity of the Montreal River. In the vicinity of St. Ignace Island (south of Nipigon Bay) lake trout would appear in pound nets during the 1st wk in June and remain until mid-July; the peak period for large individuals was around July 1 (see Table 3).

At scattered locations (such as in the vicinity of Thunder Cape) large lake trout would again move into shallow waters in mid-August. This second "summer run" was of neither the magnitude nor duration of the first.

During spring and summer, different size-classes of trout might characterize shoals in the same general area, diversity sometimes not easily attributed to the effects of differential fishing pressures alone. Fishermen claimed an ability to recognize different resident groups among the banks extending from Rousseau Bank (off Coppermine Point) to MacKinnon Bank (north of Cape Gargantua), and among the shoal complex between Michipicoten and Caribou Islands.

Native Lean Lake Trout Varieties Described by Fishermen

THE EARLY SPAWNERS

The small, early spawners tended to move to inshore waters in September or early October. On certain grounds these were typically gray or silver–gray, with lighter gray spots and light ventral surface; various fishermen knew them simply as "regular trout" or "little grays." At many locations in both eastern and western waters, however, the early trout were called "blacks." These were often described as having been robust and stocky, with brown–green, dark brown, or black backs, becoming somewhat lighter toward the ventral surface. Flesh coloration varied: blacks south of Coppermine Point showed reddish tones, whereas those spawning among the islands south of Nipigon Bay and on grounds about Jackfish and Port Coldwell tended to be much paler. In general, the small blacks would spawn in waters of 4.5 m (15 ft) or less. Among the islands of the Black Bay Peninsula they sought sheltered areas away from exposed lake shores.

Average weights cited for early spawners ranged from 1 kg (2.2 lb) to 2.7 kg (6 lb). Blacks frequenting inner Batchawana Bay, the Slate Islands (south of Jackfish), and Nipigon Bay tended to be smaller in size than those found along adjacent areas of the lake's main shore. Fishermen believed them to be discrete breeding groups. Native Nipigon Bay trout spawned 8–10 d later than those of the main lake, were brighter in color, and showed a greater tendency to develop fat.

River spawners composed the most obvious stocks of dark-colored trout. These were most prevalent south of the Pic River on the eastern shore, whereas none are known to have existed west of Nipigon Bay or along the American shore. Certain streams received a wide range of fish sizes. Dog River lake trout were, on the average, smaller than Montreal River trout (also noted by Loftus 1958), and Pukaskwa River fish could range to 9 kg (20 lb).

Although there is no evidence that more than one stock visited a single stream, streams might contain a number of separate spawning sites. The Michipicoten River, for example, showed extensive lake trout movements, occasionally extending as far as Scott Falls, 16 km (10 mi) upstream.

There is some evidence that certain river-spawning stocks (such as those of the Steel, Black or Aquasoban, and Little Pic rivers) were depleted prior to the advent of the sea lamprey (Goodier 1981). Excessive poaching was the most likely

cause, although log rafting and channel modification by storms may have had minor impacts.

Redfins and Yellowfins

In general, any lake trout possessing brightly colored fins was liable to be designated "redfin." But the name was also employed by many Lake Superior fishermen to define a specific run which followed that of the earliest spawners. It is possible that falling water temperatures could trigger fin coloration in certain fish, thus creating the illusion of a new run. However, although blacks (or "regular trout") and redfins might spawn on the same grounds, the two forms generally were not found spawning at the same time. At certain locations the retreat of the black trout would precede the arrival of redfins. The classification "redfin" has also been employed by fishermen of Isle Royale (Rakestraw 1968) and the Keweenaw Peninsula (Organ et al. 1978). Fishermen of Georgian Bay identified redfins as their second run of lake trout (Kerr 1886; Loftus 1980).

Redfins were a heavier fish than the earliest spawners. South of Michipicoten Bay redfins were reported to be paler and more elongated than blacks. Between Coppermine Point and Cape Gargantua most grounds were situated on offshore shoals, although north and south of this region many main shore grounds existed. At the Clay Banks and Shingles of Michipicoten Island, large redfins were especially abundant and fishermen believed these to remain in this vicinity all year long.

Former fishermen of the Jackfish and Port Coldwell areas tended to refer to the fish of the second run as yellowfins rather than redfins. Flesh colors were variously reddish or pale. (One fisherman reported a yellow-finned "racer" form (see section on Caribou Island and Superior Shoal lake trout) in the Jackfish Bay area.) Likewise, fishermen of the Black Bay Peninsula–Thunder Bay area would not distinguish redfins and yellowfins as different spawning classes. However, certain grounds, particularly along windward island shores, were frequented predominantly by lake trout with yellow fins. (Large colorful trout might also be described simply as "big blacks.")

Two fishermen familiar with the island shores south of Nipigon Bay and Rossport believed yellowfins to be a unique run at certain sites. Reportedly, these fish were elongated like redfins, but proportionately deeper of body, with yellow–white or white rather than red flesh. Spawning depths varied but often exceeded those of earlier-spawning lake trout.

The Late Spawners

Fishermen west of Marathon tended to perceive a greater number of discrete trout runs than fishermen to the east. Former residents of Jackfish and Port Coldwell refer to "salmon-trout," the large fish arriving after the second run. These commenced spawning in late October and in certain years continued through the month of November and into December. One interviewee described them as "... Streamlined with a small head like a West Coast salmon. The tail was not too big, and all possessed red flesh. They did not have colored fins, and they had a silvery body, not as dark as the blacks and yellowfins. Salmon-trout were taken in a little deeper water at 5 or 6 fathoms."

Fishermen of the Black Bay Peninsula knew large, red-fleshed trout as "red trout," a general category probably including a number of stocks and size-classes more or less intermingling on their grounds during the second half of the fall.

Rossport fishermen applied the name red trout to a seemingly discrete stock. Thomson (1883) also refers to this fish the Indians knew as "Pugwashooaneg, that is Pays-platt District fish, as it is taken only in this locality, and only in the fall of the year as a rule." Red trout would first appear in nets set around August 15 in 18 m (60 ft) to 36 m (120 ft) of water, thus preceding black trout into shallow waters (but actually spawning at a later date, somewhat prior to redfins and yellowfins). Although the variety could be seen on the same grounds as the blacks, their spawning sites, as indicated by fishermen, tended to be smaller in area and less numerous. Red trout were paler and heavier, and typified by red flesh.

West of Schreiber the latest spawners ran to large sizes and were known to some fishermen as gray trout. Rossport fishermen would occasionally set gill nets of 23-cm (9-in) or 25-cm (10-in) mesh for those fish of truly massive proportions (McNab 1922). Grays tended to spawn at 9 m (30 ft) to 20 m (65 ft), relatively greater depths than those preferred by most other forms of lean lake trout. It was the habit of certain stocks of grays (and less frequently yellowfins) to spawn over beds of filamentous green algae, designated "moss" by local fishermen (and identified in Lake George, New York, by Needham et al. (1922) as *Dichtomosiphon tuberosus*, with best development at an average of 14 m). Moss spawners were present at Prince Bay (south of Thunder Bay), north of Caribou Island (in Thunder Bay), near Rossport, and in Thompson Channel (north of Pic Island). At the last location, grays were abundant but absent from neighboring sites. In Michigan State waters "channel salmon" selected similar substrates in harbor areas of Isle Royale and so earned the additional nickname "moss trout." In the Michigan State waters of Lake Michigan, Organ et al. (1978) report an even greater prevalence of moss trout than in Lake Superior.

Caribou Island and Superior Shoal Lake Trout

In addition to the inshore trout runs discussed above, mid-lake shoal zones also supported apparently discrete stocks (whose members were often dark and frequently large). The native leans of Caribou Island, for example, possessed white flesh, a dark brown–green back, gray ventral region, numerous dark spots, and usually lacked colored fins. Spawning in October, they tended to be somewhat heavier than the inshore black trout. Among these Caribou Island "blacks," fishing tugs would net perhaps 2–3% gray (or silver–gray) trout with red or pink flesh, possibly individuals which had strayed from outside areas. There existed recognizable differences between the native lake trout of Michipicoten Island, Caribou Island, and the shoals and banks between these two islands.

In general, the lean lake trout of both Superior Shoal and the Bateau Rock shoals tended to have dark brown backs, mottled appearance, red-colored fins, and deep red flesh. At the former location, a number of banks rise like pinnacle mountains from the lake bottom. It is the opinion of fishermen that specific trout stocks were associated with the different

banks, effectively separated from each other by deep ditches in between. When commercial fishing developed here in the 1920s and 1930s, the individuals of some (but not all) banks were of poor condition and afflicted by a high incidence of deformities. Such fish were known as "racers." Overcrowding and a poor forage base may have been their causes. By the 1960s the frequency of deformities was considerably less; possibly population pressures had been alleviated by the fishery. (A comparable improvement in the condition of Lake Nipigon lake trout also occurred during the early decades of that lake's fishery (King, undated).)

Sand Trout

In the southeastern portion of the lake, some fishermen recognized not only two major spawning runs but also another group named "sand trout." Also designated "silver trout," this fish was slender and small, with red meat and light silvery coloration marked by darker blotches on the dorsal surface. According to two sources, the sand trout was a shoal fish, usually taken over sandy bottom depths of ~55 m (180 ft). Others knew the form to move to inshore flats in June and July. It was possibly analogous to the variety known to Lake Huron fishermen as "summer trout," which Kennedy (1941) describes as "... lighter in colour than the Winter Trout (fall-spawners). Fishermen say they have taken them with spawn running in summer. These fish "disappear" in autumn or winter." Summer trout and sand trout may have represented young age-classes (Canada Department of Marine and Fisheries 1904) and should not be regarded as stocks. Dryer (1966) located the greatest spring and summer concentrations of small lake trout in the Apostle Island region of Lake Superior between 49 m (160 ft) and 71 m (234 ft). On the other hand, sand trout may have been a seasonal phenotypic variation in certain groups of small, early spawners. Only a few sand trout spawning sites were reported by fishermen (Fig. 1). Loftus (1952) reported spawning at the Pukaskwa Flats area between October 20 and November 30, a late run for that area.

Siscowets, Half-breeds, and Paperbellies

Lake trout of high fat content were first described by the Jesuits at their Michilimackinac outpost on Lake Huron (Jesuit Relations 1670–71). Fat trout in Lake Superior were also known as siscowets, a name deriving from an Ojibway Indian word meaning "cooks itself" (Goode 1884). Inconclusive evidence exists to suggest that phenotypically distinct stocks of siscowets flourished within the lake. It was common in the early days of the fishery to distinguish two forms based on differences in skin and flesh coloration (Kingston 1853; Sweeny 1890). Barnston (1874) describes a fish known as "bear trout," fatter than siscowet with white meat of inferior quality. Isle Royale fishermen netted both black and white siscowets. "Black generally run almost three times as large as white. Spawn in up to 100 fathoms of water" (Rakestraw 1968). Fishermen interviewed usually described a single general phenotypic form, with pale pink or white flesh and body lighter in appearance than the lean lake trout. The body below the lateral line was yellowish, fading to grayish-white on the ventral surface; above it was a pale brownish-gray or greenish-brown. Spotting varied but was usually less distinct than that of leans. Authors have recorded a large range of observed body weights (Table 3). Fishermen have long noted that the deeper they fished the fatter lake trout became, and some truth undoubtedly lies in the statement of Eddy and Surber (1960) that "all sorts of gradations in body forms occur."

Only a minority of interviewees actively sought the nonlean categories of lake trout, and even these men were generally unaware of spawning locations and times. Spawning tended to occur at great depths and at times of the year when inclement weather would discourage open-lake fishing. In consequence, only general fishing areas and seasons are outlined in Fig. 1–3. Any known spawning activities are explicitly noted. A short regional summary of grounds follows.

In August siscowets spawned on the offshore banks between Coppermine Point and Cape Gargantua at 46 m (150 ft). To the north large siscowets moved onto Isacor and East Banks by mid-October and dominated the catches. Fat trout grounds also existed closer to Michipicoten Bay, but their exact location is not known (Landon 1973). In former years it was not unusual to capture fat trout in June or early July in waters less than 10 m (33 ft) near the Michipicoten River. But spring abundances were never as great here as off the Pic River, where, in the first half of the 19th century, siscowets outnumbered lean trout in the seines and shallow gill nets of the Hudson's Bay Company's Pic Post. (Several old-timers interviewed at Heron Bay and Marathon had no experience of this annual inshore movement, however.)

Close to the fishing village of Port Coldwell, Uncle Bobs Bank and banks in the vicinity of Fred Shoal were considered among the best grounds in the region. Siscowets were fished in water greater than 110 m (360 ft) until August, when nets were moved to the edges of the various banks. Purvis (1977) was informed by local fishermen that fats came to the banks east of Pic Island to spawn at this time. However, in years past, the Nicoll Brothers Fishery of Port Coldwell was unable to procure fat trout spawn for the Port Arthur Hatchery until November and December (Nicoll 1917, 1920).

Large siscowets ranged along the length of Pic Bank. Reportedly, spawning occurred on the Copper Island Bank from September 1 to early November. In July pound nets set at certain points along the outside island shores south of Rossport would take fats, while occasionally trolling would also prove successful. To the west, along the Black Bay Peninsula, nets could be sunk at various locations on the dropoff of the island shoals to capture siscowets and half-breeds (although nonleans were never intensively fished in this region). In Thunder Bay itself siscowets were occasionally sought in the central basin in November or off Clavet Bay in August.

It is thought that half-breeds are immature fat trout (Khan and Qadri 1970), although some fishermen refute this and claim to have found them in spawning condition. Half-breeds were fished at shallower depths than fats, and there existed certain popular grounds where they were netted in greatest abundance. For smoking purposes this variant was usually preferred over siscowets.

Paperbellies, known to American fishermen as humpers, have been described by Eschmeyer and Phillips (1965), Rahrer (1965), and Patriarche and Peck (1970). They are

unique in having a very white ventral region, sometimes distended, with abnormally thin skin. Paperbellies are a lighter gray than the deep-water siscowets. It has been suggested by Lawrie and Rahrer (1973) that the variant derives from wandering lean lake trout, which colonized the offshore banks and underwent subsequent polymorphic development. Paperbellies were reported to have existed on all the banks between Caribou and Michipicoten Islands and were especially abundant on the flat, northernmost bank of Superior Shoal. According to one fisherman, around June 1 of each year there occurred inshore movements of paperbellies to the vicinity of Port Coldwell harbor.

Conclusion

The criteria employed by fishermen in recognizing "breeds" of lake trout can provide useful background information for researchers interested in stock identification. Prior to 1955, there existed in Lake Superior visibly different spawning groups or runs of lean lake trout, apparently separable in terms of time and/or space. Regional trends in spawning periods evident on a large scale were no doubt partly related to water temperature differences. Local variations, however, suggest the sympatric association of various breeding stocks. It is probable that the sedentary nature of certain lake trout groups, both lean and nonlean, encouraged stock formation, especially on offshore shoals. Other groups, although highly migratory at spawning time, probably maintained strong homing tendencies which could encourage segregation (see review in Lawrie 1978; Martin and Olver 1980). This was most apparent among the river-spawning lake trout populations of the east and northeast shores. In addition, certain groups, although mixing more or less freely on the shore or shoal grounds, evidently remained semidiscrete, for they were seen year after year at the same locations.

It is the nature of the sources used in an historical approach such as this that an abundance of clues for mapping former fish stocks is generated: unfortunately, many must also remain speculative and inconclusive. Further analyses (including electrophoretic techniques) of stock remnants would prove valuable in both verifying fishermen's impressions and determining degrees of stock discreteness (see, for example, Dehring et al. 1981). Surviving stocks of native lean lake trout have been reported at the Slate Islands, Bateau Rock, and Pie Island. In addition, genetic strains of Lake Superior trout have been maintained for many years in a number of Ontario's inland lakes (such as Killala and Mishibishu lakes), as well as in the breeding tanks of several Ontario fish hatcheries. In fact, during the past 100 yr Lake Superior has been a popular source of transplants, which have been scattered widely about North America.

The havoc wrought by the sea lamprey on the salmonid stocks of the Great Lakes has been well documented. It has been suggested by Lawrie and Rahrer (1973) that a sequential fishing-up process of lake trout stocks was occurring within Lake Superior waters prior to the advent of *P. marinus*. The opportunistic development of the commercial industry created conditions in which this would be likely to occur. On the basis of both the interviews and preliminary examination of government reports prior to 1940, the contention of the above authors seems to be valid for some regions. (The apparent depletion of river-spawning stocks is mentioned above, for example.)

Reviewing the processes of stock transformation and loss within the lake should be the next step for continued research. Again, the primary and most valuable sources of information are the "old-timers" themselves, fishermen who have repeatedly demonstrated an intimate awareness of lake conditions and fish habitats. Such knowledge develops only from years of observation, from the certainty that economic and physical security depends on its accurateness, and from a respect for, and desire to conserve, the environment which has lent them a livelihood.

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Survey of the Genetic Variation Among Eastern Lake Superior Lake Trout (*Salvelinus namaycush*)[1]

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Patterns of genetic variation among lake trout (*Salvelinus namaycush*) of eastern Lake Superior were examined using starch gel electrophoresis. We used 484 individuals sampled from three areas, representing three morphological types (leans, humpers, and siscowets). Of 50 loci examined, 44 were monomorphic in all groups sampled. Genetic variation occurs at six loci AAT-1,2, MDH-3,4, ME-1, and SOD-1. The average heterozygosity found ($H = 0.015$) is low relative to other salmonid species. A significant amount of heterogeneity exists among the 10 lake trout samples. These differences are due to variation within as well as between morphological types. The significance and management implications of these data are discussed.

Key words: genetic variation, lake trout, *Salvelinus namaycush*, Lake Superior

DEHRING, T. R., A. F. BROWN, C. H. DAUGHERTY, AND S. R. PHELPS. 1981. Survey of the genetic variation among eastern Lake Superior lake trout (*Salvelinus namaycush*). Can. J. Fish. Aquat. Sci. 1738–1746.

L'électrophorèse sur gel d'amidon a été utilisée pour étudier les caractéristiques de la variation génétique chez les touladis (*Salvelinus namaycush*) de l'est du lac Supérieur. Nous avons utilisé 484 sujets provenant de trois régions, représentant trois types morphologiques (« maigres », « bossus » et « siscowets »). Des 50 loci examinés, 44 sont monomorphes dans tous les groupes échantillonnés. Il y a variation génétique à six loci, AAT-1,2, MDH-3,4, ME-1 et SOD-1. Comparée à celle d'autres espèces de salmonidés, l'hétérozygosité moyenne observée ($H = 0{,}015$) est relativement basse. Parmi les 10 échantillons de touladis, il existe un degré significatif d'hétérogénéité. Ces différences sont dues à la variation aussi bien inter qu'intratypes morphologiques. Nous analysons la signification et les implications de ces données pour la gestion.

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SEVERAL forms of lake trout (*Salvelinus namaycush*) are phenotypically distinguishable in Lake Superior. It has been suggested that as many as a dozen subgroups or stocks of lake trout may exist in Lake Superior (Eschmeyer 1957). The three most commonly recognized morphotypes are addressed in this paper: Lean lake trout (leans); humpers (humpies, paperbellies, or bankers); and siscowets (fats or fat trout). Many morphological differences are recognized between these forms (Crawford 1966; Eddy 1969; Eschmeyer 1955, 1957; Eschmeyer and Phillips 1965; Hubbs and Lagler 1958; Khan and Qadri 1970; Lawrie and Rahrer 1973; Patriarch and Peck 1970; Rahrer 1965; Thurston 1962). There is also a large amount of variation and overlap in these characteristics which makes it difficult to identify the morphotype of some specimens (Khan and Qadri 1970).

To date there have been few attempts to determine the genetic basis, if any, for the morphological differences or to survey the genome of lake trout for population differences. Data of this nature would have valuable management implications. This type of data could be used by managers to define the management units of lake trout (i.e. as a lake, a restricted area, or a stock). A lack of understanding of the lake trout population structure may be responsible for the unsuccessful attempt at reestablishing self-sustaining populations of lake trout in the lower Great Lakes (Loftus 1976). Genetic data obtained through electrophoretic analysis has been useful in describing the population structure of salmonid species (Allendorf et al. 1976, 1977; Bouch and Ball 1968; Eckroat 1971, 1973; Huzyk and Tsuyuki 1974; Reinitz 1977; Tsuyuki and Roberts 1965; Tsuyuki et al. 1966; Utter and Hodgins

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TABLE 1. Net data for each sample in Lake Superior.

Code[a]	Area		Date lifted	Length (m)	Stretch mesh (cm)	Depth (m)	Types caught
	Latitude	Longitude					
SN	47°14′	87°05′	May 11	1830	11.4	42–58	Leans
SS	47°10′	87°16′	May 11	1830	11.4	42–58	Leans
SN	47°14′	87°05′	May 14	1830	11.4	110–165	Leans/Humpers/Fats
RS	48°04′	88°34′	May 23	915	11.4	42–58	Leans/Humpers
RR	48°08′	88°26′	May 23	3658	11.4	64–82	Leans/Humpers
CI	47°14′	85°54′	May 26	5485	11.4	44–172	Leans/Humpers/Fats

[a]SN, Stannard Rock north set; SS, Stannard Rock south set; RS, Isle Royale south set; RR, Isle Royale Rock Harbor set; CI, Caribou Island set.

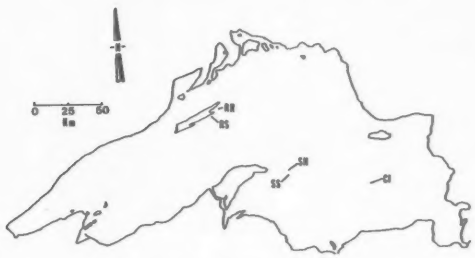

FIG. 1. Location of net sets in Lake Superior. RR: Isle Royale, Rock Harbor set; RS: Isle Royale, shore set; SN: Stannard Rock, north set; SS: Stannard Rock, south set; CI: Caribou Island set.

1972; Utter et al. 1973b) and its importance as a management tool has been recognized (Behnke 1972; Ihssen 1976; Larkin 1972; Loftus 1976). While electrophoretic techniques have been successfully applied to many salmonid species, lake trout have received limited attention (May et al. 1979, 1980; Patriarch and Peck 1970; Tsuyuki et al. 1966; Wuntch and Goldberg 1970).

In this study we have attempted to survey the genome and document genetic variability in sample groups of lake trout in eastern Lake Superior. This genetic variation may have potential management use as biochemical genetic markers (Moav et al. 1976, 1978; Utter et al. 1974), and help in defining the basic management unit of lake trout.

Methods and Materials

Lake trout were collected between May 11 and 26, 1979, at five locations in Lake Superior: Stannard Rock (two locations), Isle Royale (two locations), and the southwest banks of Caribou Island (one location) (Table 1 and Fig 1). A total of 484 fish representing 10 sample groups were collected by commercial fishermen using gill nets. Individual fish were assigned to these groups of the basis of morphotype and the location of capture. Fish heads were removed and labeled with a numbered spaghetti tag, placed on ice, and transported to Northern Michigan University. Samples of liver, epaxial muscle, and eye (vitreous) fluid were removed and frozen (−40°C) until electrophoretic analysis.

Starch gel electrophoresis of the samples was conducted at the University of Montana using the techniques of Utter et al. (1974) and Allendorf et al. (1977). The genic nomenclature used in this study was proposed by Allendorf and Utter (1979) and May et al. (1979).

Results and Discussion

GENETIC VARIATION

We examined 25 enzymes that were coded for by 50 loci (Table 2). An additional 20 loci were observed but not scored because of poor resolution or activity, inconsistent results, or because the variation observed could not be explained genetically (Dehring 1981). Genetic variation occurred at four of the enzymes scored. The loci coding for the enzymes are AAT-1,2, MDH-3,4, ME-1, and SOD-1.

Inheritance studies (controlled matings) to confirm the genetic basis of the variable isozyme patterns of lake trout is lacking. These studies have been carried out, however, on brook trout (*Salvelinus fontinalis*) and rainbow trout (*Salmo gairdneri*). At AAT-1,2 we found isozyme patterns characteristic of a duplicated locus. Studies on brook trout indicate that similar variation at these loci is genetically controlled by two loci acting as a single duplicate locus (May et al. 1979; Wright et al. 1980). We used muscle tissue to screen for variation at MDH. Our data show duplication and variation at MDH-3,4, consistent with that observed in brook trout (May et al. 1979). At ME we have evidence of only two muscle loci, which differs from brook trout data (Stoneking et al. 1979). It is possible that two loci products have the same mobility at this activity zone and only one is variable. However, we did not record enough variation at the variable locus to determine the presence of one or two loci. At SOD we recorded a slow allele. Genetic variation in lake trout for this enzyme was not reported by May et al.(1979). The mobility of this slow allele is faster than the common allele in brook trout (B. May, personal communication). This allelic variant followed the same pattern as that observed in rainbow trout (Utter and Hodgins (1972).

One of the most common measures of genetic variation is the average heterozygosity (H), the average proportion of heterozygous individuals per locus (Avise 1975). The average detectable heterozygosity has been completed for each morphological group and for all the lake trout used in the analysis (Table 3). It is computed over all loci examined (50). The average heterozygosity for the lake trout sampled is low ($H = 0.015$) when compared with other salmonids (Allen-

TABLE 2. Designation of loci coding for each enzyme. Buffer systems and tissues used for each locus and alleles identified are shown. L = liver; M = muscle; E = eye fluid; I = Ridgway (Ridgway et al. 1970) II = Clayton and Tretiak (Clayton and Tretiak 1972).

Enzyme	Abbreviation	Buffer system	Tissue used	Loci and alleles identified
Aspartate aminotransferase	AAT	I	M	*AAT-1,2* (100,85)
Adenylate kinase	ADK	II	L	*ADK-3* (100)
		I	E	*ADK-4* (100)
Alpha-glycerophosphate dehydrogenase	AGP	I	L	*AGP-1* (100)
		II	M	*AGP-2* (100)
		I	L	*AGP-3* (100)
Aldolase	ALD	I	L	*ALD-1* (100)
		I	L	*ALD-3* (100)
Creatine phosphokinase	CPK	II	M	*CPK-1* (100)
		II	M	*CPK-2* (100)
Esterase	EST	I	L	*EST-1* (100)
Fructose-1,6-diphosphatase	F-1,6-DP	I	L	*F-1,6-DP-1* (100)
		II	M	*F-1,6-DP-3* (100)
Fumarase	FUM	I	E	*FUM-1* (100)
		I	E	*FUM-2* (100)
Glyceraldehyde-3-phosphate dehydrogenase	GAPDH	II	L	*GAPDH-1* (100)
		II	L	*GAPDH-3* (100)
		II	L	*GAPDH-4* (100)
Glutamate dehydrogenase	GDH	I	L	*GDH-1* (100)
		I	L	*GDH-2* (100)
Glucose-6-phosphate dehydrogenase	G-6-PDH	I	M	*G-6-PDH-1* (100)
		I	M	*G-6-PDH-2* (100)
Hexokinase	HK	II	L	*HK-1* (100)
Isocitrate dehydrogenase	IDH	II	M	*IDH-1* (100)
		II	M	*IDH-2* (100)
		II	M	*IDH-3,4* (100)
Leucine aminopeptidase	LAP	II	E	*LAP-1* (100)
Lactate dehydrogenase	LDH	I	M	*LDH-1* (100)
		I	M	*LDH-2* (100)
		I	M	*LDH-3* (100)
		I	M	*LDH-4* (100)
		I	E	*LDH-5* (100)
Malate dehydrogenase	MDH	I	M	*MDH-3,4* (100,170)
Malic enzyme	ME	II	M	*ME-1* (100,115)
		II	M	*ME-2* (100)
Peptidase	PEP	I	L	*PEP-1* (100)
6-phosphogluconate dehydrogenase	6-PGDH	II	L	*6-PGDH-2* (100)
		II	M	*6-PGDH-3* (100)
Phosphoglucose isomerase	PGI	II	M	*PGI-1* (100)
		II	L	*PGI-2* (100)
		II	E	*PGI-3* (100)
Phosphoglucomutase	PGM	II	L	*PGM-1* (100)
		II	L	*PGM-2* (100)
Phosphomannose isomerase	PMI	II	L	*PMI-1* (100)
Sorbitol dehydrogenase	SDH	I	L	*SDH-1* (100)
Superoxide dismutase	SOD	I	L	*SOD-1* (100,85)
Xanthine dehydrogenase	XDH	I	L	*XDH-1* (100)

TABLE 3. Average detectable heterozygosity (H) and standard error (SE).

Morphotype	No. of fish sampled	$H \pm$ SE
Leans	150	0.014±0.004
Humpers	230	0.014±0.003
Siscowets	93	0.016±0.003
Total eastern Lake Superior lake trout	473	0.015±0.003

dorf and Utter 1979). However, the H values obtained for lake trout are comparable with those observed for *Oncorhynchus* species, e.g. coho salmon ($H = 0.015$), and sockeye salmon ($H = 0.018$) (Allendorf and Utter 1979; Utter et al. 1973a). The low H value obtained in this study may be due to the large number of monomorphic loci that we used, which are not generally scored in other studies. The H value could increase if several of the variable loci not used could be reliably interpreted. A low level of heterozygosity may adversely affect the ability of lake trout to adapt to a new environment or changing environmental conditions (Krueger et al. 1981).

TABLE 4. Distribution of genotypes and allele frequencies at AAT-1,2.

Sample group[a]	No. of fish	100/100/ 100/100	100/100/ 100/85	100/100/ 85/85	100/85/ 85/85	85/85/ 85/85	AAT-1,2(100)±C.I.[b]
SSL	50	5	7	25	12	1	0.52±0.07
SNL	40	7	9	13	6	5	0.54±0.08
SNH	45	25	11	7	1	1	0.82±0.06
SNF	38	15	15	5	3	0	0.78±0.06
RSL	2	0	1	0	1	0	0.50±0.35
RSH	31	10	6	6	7	2	0.62±0.08
RRH	7	0	0	4	3	0	0.39±0.18
CIL	23	1	9	7	3	3	0.52±0.10
CIH	80	17	20	26	14	3	0.61±0.05
CIF	37	9	12	8	7	1	0.64±0.08

[a]SSL, Stannard Rock leans south set; SNL, Stannard Rock leans north set; SNH, Stannard Rock humpers north set; SNF, Stannard Rock siscowets north set; RSL, Isle Royale leans shore set; RSH, Isle Royale humpers shore set; RRH, Isle Royale humpers Rock Harbor set; CIL, Caribou Island leans; CIH, Caribou Island humpers; CIF, Caribou Island siscowets.
[b]C.I., confidence interval.

TABLE 5. Distribution of genotypes and allele frequencies at MDH-3,4[a]

Sample group	No. of fish	100/100/ 100/100	100/100/ 100/170	100/100/ 170/170	100/170/ 170/170	170/170/ 170/170	MDH-3,4(100)±C.I.
SSL	49	44	2	3	0	0	0.96±0.03
SNL	47	39	4	3	1	0	0.93±0.04
SNH	47	40	6	1	0	0	0.96±0.03
SNF	45	42	3	0	0	0	0.98±0.02
RSL	8	7	1	0	0	0	0.97±0.06
RSH	76	54	22	0	0	0	0.93±0.03
RRH	11	7	4	0	0	0	0.91±0.08
CIL	28	24	4	0	0	0	0.96±0.04
CIH	95	69	25	0	1	0	0.93±0.03
CIF	44	29	13	2	0	0	0.90±0.04

[a]Abbreviations same as those in Table 4.

TABLE 6. Distribution of genotypes, χ^2 test for agreement with Hardy–Weinberg proportions (1 df), and allele frequencies at ME-1 (*Significant at $P = 0.01$.)[a]

Sample group	No. of fish	100/100	100/115	115/115	χ^2	ME-1 (100)±C.I.
SSL	50	50	0	0	0.00	1.00
SNL	48	47	1	0	0.00	0.99±0.02
SNH	47	45	2	0	0.02	0.98±0.03
SNF	45	14	31	0	12.40*	0.66±0.10
RSL	8	8	0	0	0.00	1.00
RSH	75	69	6	0	0.13	0.96±0.03
RRH	11	11	0	0	0.00	1.00
CIL	28	25	3	0	0.05	0.95±0.06
CIH	96	91	5	0	0.07	0.97±0.02
CIF	46	44	2	0	0.02	0.98±0.03

[a]Abbreviations same as those in Table 4.

GENETIC VARIATION WITHIN SAMPLES

We computed the observed genotype distribution, χ^2 values for agreement with Hardy–Weinberg equilibrium values, and gene frequencies of each sample group (Tables 4–7). A χ^2 test for agreement with Hardy–Weinberg proportions was not applied to the duplicated loci, AAT-1,2 and MDH-3,4 because of difficulties in assigning alleles to a locus (Allendorf and Utter 1979; Imhof et al. 1980).

We observed genotypic proportions in agreement with Hardy–Weinberg expectations for most populations; however, a few deviated significantly. Stannard Rock siscowets (SNF) deviated significantly from the expected at ME-1 because of an excess of heterozygotes. This may be due to duplication of this locus as reported by Stoneking et al. (1979) in *Salvelinus* and our inability to differentiate different doses

TABLE 7. Distribution of genotypes, X^2 test for agreement with Hardy–Weinberg proportions (1 df), and allele frequencies at SOD-1. (*Significant at $P = 0.01$.)[a]

Sample group	No. of fish	100/100	100/85	85/85	χ^2	SOD-1 (100)±C.I.
SSL	50	45	5	0	0.14	0.95±0.05
SNL	48	39	8	1	0.55	0.90±0.06
SNH	47	46	0	1	47.00*	0.98±0.03
SNF	47	46	1	0	0.00	0.99±0.02
RSL	8	8	0	0	0.00	1.00
RSH	75	61	13	1	0.10	0.90±0.05
RRH	11	10	1	0	0.02	0.95±0.09
CIL	28	28	0	0	0.00	1.00
CIH	97	84	13	0	0.50	0.93±0.04
CIF	46	43	3	0	0.05	0.97±0.03

[a]Abbreviations same as those in Table 4.

TABLE 8. Comparison of finclipped and non-finclipped lean lake trout captured at Caribou Island. (*Significant at $P > 0.01$.)

Isoyzme	Genotype distribution					P	χ^2
AAT-1,2	100/100/ 100/100	100/100/ 100/85	100/100/ 85/85	100/85/ 85/85	85/85/ 85/85		
Finclipped	4	3	5	1	1	0.64	2.08
Non-finclipped	1	9	7	3	3	0.52	
MDH-3,4	100/100/ 100/100	100/100/ 100/170	100/100/ 170/170	100/170/ 170/170	170/170/ 170/170		
Finclipped	15	1	0	0	0	0.98	0.60
Non-finclipped	24	4	0	0	0	0.96	
ME-1	100/100		100/115		115/115		
Finclipped	16		0		0	1.00	1.77
Non-finclipped	25		3		0	0.95	
SOD-1	100/100		100/85		85/85		
Finclipped	12		3		1	0.84	9.28*
Non-finclipped	28		0		0	1.00	

of the alternate (115) allele. Stannard Rock humpers (SNH) and Caribou Island leans (CIL) deviate significantly from Hardy–Weinberg expected proportions at SOD-1. The leans at Stannard Rock had several variants at SOD-1, while the humpers (SNH) had only one variant homozygous for the alternate (85) allele. It is possible then, that the significant χ^2 value for SNH may be due to a small lean lake trout morphologically misidentified as a humper. The lean trout caught at the Caribou Island location included a high percentage of planted (finclipped) fish. The significant deviation obtained for this group was due to a deficit of heterozygotes. Consequently, when the CIL sample group was subdivided into finclipped and non-finclipped groups, a χ^2 test (2×2 contingency) revealed a significant difference between the groups at SOD-1 ($\chi^2 = 9.98$, $P < 0.01$, Table 8). This indicates that the planted lake trout may be genetically different from the native leans at Caribou Island. Therefore, only non-finclipped fish will be considered in analyzing the population structure of the eastern Lake Superior lake trout.

GENETIC VARIATION BETWEEN SAMPLES

To examine whether the lake trout sampled in eastern Lake Superior represent a single random mating population or distinct stocks, we compared the gene frequencies at the four polymorphic loci using allelic counts in a 2×7 χ^2 test of independence. Significant differences in gene frequency occur between the sample groups at all four polymorphic systems (Table 9). To determine how this variation is partitioned between sampling areas and morphotypes, we compared all the sample groups on a pairwise basis (2×2 χ^2 test). Significant differences were found at 30 of 89 pairwise comparisons at $P < 0.05$. These differences are evident both between the various morphotypes and between the geographic

TABLE 9. Chi-square values for independence of allele counts between sample groups (2×7 contingency table; 6 df) for lake trout of eastern Lake Superior. (*Significant at $P = 0.05$; **significant at $P = 0.01$.)

Locus	χ^2
AAT-1,2	64.84**
MDH-3,4	15.10*
ME-1	162.21**
SOD-1	12.99*

TABLE 10 (a–d). Chi-square values for differences in allelic counts at AAT-1,2; MDH-3,4; ME-1; and SOD-1. (*Significant at $P = 0.05$; **significant at $P = 0.01$.)[a]

(a) AAT-1,2

Leans	0.00						
SNH	47.66**	0.00					
SNF	29.53**	1.09	0.00				
RSH	3.55	15.46**	7.95**	0.00			
RRH	1.88	24.81**	17.12**	4.88*	0.00		
CIH	4.92*	24.86**	13.30**	0.08	4.84*	0.00	
CIF	6.08*	13.76**	6.58*	0.13	6.10*	0.54	0.00
	Leans	SNH	SNF	RSH	RRH	CIH	CIF

(b) MDH-3,4

Leans	0.00						
SNH	0.14	0.00					
SNF	3.63	2.13	0.00				
RSH	1.90	1.80	7.16**	0.00			
RRH	1.42	1.70	6.44*	0.19	0.00		
CIH	2.36	2.05	7.59**	0.00	0.17	0.00	
CIF	5.16*	4.15*	10.72**	0.88	0.01	0.85	0.00
	Leans	SNH	SNF	RSH	RRH	CIH	CIF

(c) ME-1

Leans	0.00						
SNH	0.17	0.00					
SNF	95.07**	32.62**	0.00				
RSH	2.59	0.64	39.98**	0.00			
RRH	0.33	0.48	10.48**	0.91	0.00		
CIH	0.72	0.06	55.78**	0.53	0.59	0.00	
CIF	0.19	0.00	31.92**	0.59	0.49	0.05	0.00
	Leans	SNH	SNF	RSH	RRH	CIH	CIF

(d) SOD-1

Leans	0.00						
SNH	1.87	0.00					
SNF	3.39	0.34	0.00				
RSH	2.80	5.53*	7.53**	0.00			
RRH	0.04	0.41	1.28	0.68	0.00		
CIH	0.24	2.68	4.35*	1.23	0.15	0.00	
CIF	0.79	0.23	1.07	3.76	0.09	1.40	0.00
	Leans	SNH	SNF	RSH	RRH	CIH	CIF

[a]Abbreviations same as those in Table 4.

locations sampled (Table 10, a–d). These data indicate that a high degree of heterogeneity exists among the sample groups and that genetically distinct groups of lake trout exist within eastern Lake Superior.

The fish were collected in May and were not spawning at that time, so we cannot conclude that the groups studied represent actual breeding populations. However, by comparing morphotype sample gene frequency data with life history data, we can get an indication of the reproductive relationships of our samples. When compared on a pairwise basis, few significant differences were found between any of the lean sample groups. When combined, the observed genotype distribution agrees with that expected of a normal Hardy–Weinberg distribution for ME-1 and SOD-1. We suggest several explanations for this. (1) Mark and recapture data indicate that leans tend to home to specific breeding sites to spawn, but disperse with their greatest mixing occurring in the spring (Eschmeyer et al. 1953). The excessive mixing in the spring would cause Lake Superior lean populations to appear as a homogeneous group. (2) The leans may form one large panmictic population. (3) Leans may form semidiscrete "demes" but do not all home true to natal spawning grounds, therefore there may be enough gene flow between populations to keep allele frequencies similar. Because the lean sample groups cannot be differentiated, they will be lumped into one group (leans) for comparisons with other sample groups.

In contrast to the leans, mark and recapture data for humpers indicate no significant movement to the shore banks or to contiguous reefs, even over extended periods of time (Lawrie and Rahrer 1973). Our electrophoretic data indicate the same trend. The two humper sample groups from Isle Royale (RSH and RRH) differ significantly at AAT-1,2 (Table 10a). Also, all the humper sample groups differ significantly from each other at one or more loci, with one exception (RSH and CIH). Because of these differences, we conclude that the sample groups collected are apparently stocks.

There are no known mark and recapture data for siscowets. Our electrophoretic data indicate the two siscowet groups (SNF and CIF) differ significantly at three of the four poly-

TABLE 11. Genetic identities (Nei's *I*) between sample groups

Leans	1.0000						
SNH	0.9991	1.0000					
SNF	0.9981	0.9989	1.0000				
RSH	0.9999	0.9995	0.9986	1.0000			
RRH	0.9998	0.9980	0.9971	0.9994	1.0000		
CIH	0.9999	0.9995	0.9985	0.9999	0.9995	1.0000	
CIF	0.9998	0.9996	0.9986	0.9999	0.9993	0.9999	1.0000
	Leans	SNH	SNF	RSH	RRH	CIH	CIF

morphic loci (AAT-1,2 $\chi^2 = 6.58$; MDH-3,4, $\chi^2 = 10.72$; ME-1, $\chi^2 = 31.92$). These differences indicate that the siscowets sampled form distinct groups (stocks). Because the siscowets were not spawning at the time of collection, these data would indicate that siscowets, like humpers, do not tend to disperse throughout the lake.

Morphotypes vs. Sampling Areas

Using the genetic identity measure proposed by Nei (1975), the extent of genetic similarity between different morphotypes within a sampling area can be compared to the genetic similarity between sampling areas (Table 11). From the dendrogram (Fig. 2) it is evident that there is more genetic similarity between morphotypes within a sampling area than between morphotypes from different sampling areas. This could be due to some gene flow between morphotypes at a sampling area and/or a lack of gene exchange between morphotypes from different areas (i.e. recent divergence). These reasons could also explain the high *I* values between the sample groups (Table 11).

Since completion of this study, it has been brought to our attention that some of the samples from Caribou Island may have been morphologically misidentified by the commercial fishermen (J. Peck, MDNR, personal communication). Errors of this type should obscure the actual genetic differences between morphotypes. It is probable then, that the actual genetic variation occurring between the morphotypes at Caribou Island is underestimated.

Management Implications

To manage a fish species on a stock basis, it is first necessary to identify the stocks present. For lake trout this is difficult using morphometric or meristic methods (Khan and Qadri 1970). This inability to identify distinct populations complicates the management of these fish. However, the electrophoretic data obtained in this study suggest that biochemical genetic markers in the form of allele frequency differences can be potentially useful in identifying lake trout populations. Biochemical markers are often used to determine the area where caught fish originate, or to identify the component populations of a mixed fishery catch (Utter et al. 1976; Widrig and Taft 1957). For example, sample groups RSH and RRH have significantly different AAT-1,2 (85) allele frequencies: 0.38 and 0.61, respectively. To increase the reliability of such markers, more data would be desirable. These data should be taken when the fish are spawning to ensure the identification of breeding populations.

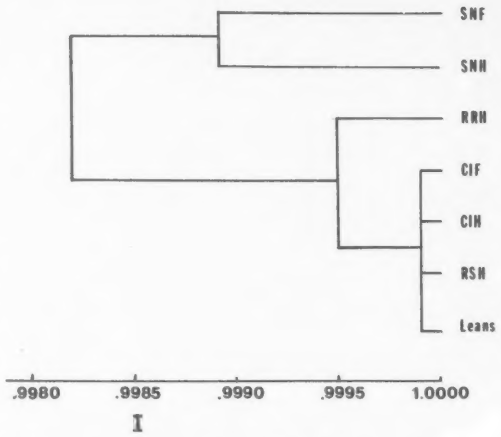

FIG. 2. Average linkage dendrogram of genetic identities for lake trout of eastern Lake Superior. Leans, combined lean trout; SNH, Stannard Rock humpers north set; SNF, Stannard Rock siscowets north set; RSH, Isle Royale humpers shore set; RRH, Isle Royale humpers Rock Harbor set; CIH, Caribou Island humpers; CIF, Caribou Island siscowets.

Where they occur together, hybridization of native and planted stocks could result in a disruption of adaptive gene pools (Krueger and Menzel 1979; Loftus 1976). As noted earlier, the native leans at Caribou Island differed significantly from the planted fish there. Thus it appears the fish being planted are possibly genetically different. The effect of this is on the lake trout's adaptive gene pool is uncertain.

Conclusion

By using the electrophoretic data obtained in this study, we cannot differentiate between individual fish on the basis of sample area or morphotype. On a lakewide basis, the 2×7 χ^2 independence test (Table 9) indicates that lake trout do not form a homogeneous group. On a sample group basis, 2×7 χ^2 for differences in allelic counts (Table 10a–d) indicate many significant differences. These data strongly indicate a high degree of heterogeneity of lake trout within eastern Lake Superior. This important conclusion warrants further study of lake trout in Lake Superior to identify the stocks present for management purposes and to help in the efforts to rehabilitate lake trout in the Great Lakes.

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Historical Evidence for Discrete Stocks of Lake Trout (*Salvelinus namaycush*) in Lake Michigan[1,2]

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Although few biological data exist on the now extinct native lake trout, *Salvelinus namaycush*, of Lake Michigan, historical records and interviews with former commercial fishermen strongly suggest that this once widespread resource was composed of a number of discrete spawning populations or stocks. A natural division of the resource into distinct stocks is consistent with the size of Lake Michigan and its varied physiography. The native trout may have undergone subtle genetic changes over the millennia, although we cannot determine whether the physical and behavioral differences represented different genotypes or only temporary effects of the local environment. Because of physiographic similarities among the upper Great Lakes and probable interchanges of lake trout during the last glacial period, we recommend that progeny of extant wild stocks, particularly from Lake Superior, are genetically most suitable for recolonizing Lake Michigan. Moreover, the hatchery-held parents of such fish should be infused periodically with genes of the wild or feral donor populations. Despite the sound historical basis for these recommendations, we also recognize that sufficiently high stocking rates coupled with a reduction of heavy exploitation may be even more important than heritability in obtaining self-sustaining populations.

Key words: lake trout, discrete stocks, Lake Michigan, historical changes, phenotype, homing, extinction, planted strains, rehabilitation

BROWN, E. H., JR., G. W. ECK, N. R. FOSTER, R. M. HORRALL, AND C. E. COBERLY. 1981. Historical evidence for discrete stocks of lake trout (*Salvelinus namaycush*) in Lake Michigan. Can. J. Fish. Aquat. Sci. 38: 1747–1758.

Bien qu'on dispose de peu de données biologiques sur le touladi (*Salvelinus namaycush*) indigène, maintenant disparu, du lac Michigan, les données historiques et les entretiens avec d'anciens pêcheurs commerciaux suggèrent fortement que cette ressource, jadis largement répandue, se composait de plusieurs populations ou stocks reproducteurs distincts. Une division naturelle de la ressource en stocks séparés est d'ailleurs compatible avec l'étendue et la physiographie variée du lac Michigan. A cours des millénaires, le touladi indigène peut avoir subi des changements génétiques subtils, bien que nous ne puissions déterminer si les différences physiques et éthologiques représentaient des génotypes différents ou seulement des effets temporaires de l'environnement local. À cause de similaritiés des Grands Lacs supérieurs et d'échanges probables des touladis d'un lac à l'autre durant la dernière période glaciaire, nous sommes d'avis que les descendants de stocks sauvages actuels, en particulier ceux du lac Supérieur, conviennent le mieux, au point de vue génétique, à un repeuplement du lac Michigan. En outre, les parents maintenus en pisciculture de tels poissons devraient recevoir périodiquement des gènes des populations sauvages ou férales donatrices. En dépit du solide fondement historique de ces recommandations, nous reconnaissons que des taux de

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peuplement suffisamment élevés couplés à une réduction de l'exploitation seraient encore plus importants que la transmission héréditaire pour obtenir des populations autosuffisantes.

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JUDGED by its high yields to commercial fisheries, the native lake trout, *Salvelinus namaycush*, of Lake Michigan composed the largest and most productive lake trout resource in North America (Fig. 1). Native Lake Michigan trout, like those in the other oligotrophic Great Lakes, were notable not only for their lakewide abundance and yields, but also for unusual variations in size and other physical characteristics. After more than a century of exploitation, however, the native trout, which had been so well adapted to Lake Michigan's differing environments, began a sudden, shocking decline in abundance in 1945 that led to their extinction in the late 1950s. Although investigators noted adverse effects of exploitation on local populations even in the 1800s and early 1900s (Milner 1874; Smith and Snell 1891; Smith 1908) and discerned a gradual decline in abundance in subsequent decades (Van Oosten 1949), most authorities agreed that predation by the sea lamprey, *Petromyzon marinus*, was the main cause for the lake trout's ultimate demise (Hile et al. 1951; Eschmeyer 1957). Subsequently, the large sea lamprey population in Lake Michigan was reduced to a low level with applications of a chemical larvicide in its spawning streams (beginning in 1961), clearing the way by 1965 for large-scale plantings of yearling lake trout that averaged 2.3 million fish annually during 1965–79. These hatchery-reared trout have survived reasonably well to adulthood, but have not established self-renewing populations (Kutkuhn 1981).

In inferring that the native trout in Lake Michigan included a number of discrete spawning populations or stocks, we rely on somewhat subjective historical records and recollections by fishermen of the prelamprey fisheries, on studies of other lake trout populations in North America, and on the recent performance of introduced strains. If the native stocks were still extant, we would consider possible ways for managing their harvest on a natural or stock level to ensure their continued productivity and survival. The present artificially maintained stocks, however, present a different set of circumstances. We have therefore attempted to relate our findings on the native trout to present rehabilitation problems by suggesting strategies that may help in their gradual resolution. We have also voiced concern over the widespread and premature harvesting of the planted fish that, if left uncontrolled, could make other considerations about rehabilitating and managing lake trout in Lake Michigan rather academic.

Phenotypes, Ecology and Stock Differentiation in the Native Lake Trout

The biology of indigenous lake trout of Lake Michigan went almost unstudied until the end of World War II, when predation by the sea lamprey was already becoming serious. The apparent stability of the resource, reflected in several decades of steady yields, gave no cause for alarm, and the limited funds and personnel available for fishery research on the Great Lakes were directed instead at so-called problem species (Smith 1972; Hile 1953). Because of the consequent scarcity of biological data of any kind with which to describe the native trout, we have relied on historical records such as those in reports of the former U.S. Commission of Fish and Fisheries, and on recent interviews with commercial fishermen who fished for lake trout before the species became extinct in the 1950s.

THE 1800S TO EARLY 1900S

Writers in the 19th and early 20th centuries reported that native lake trout of Lake Michigan possessed a number of distinct phenotypes, associated with behavioral differences and different habitats occupied. On the basis of a consistent pattern in these historical accounts, native trout were broadly separated into deepwater and shallow-water forms. The deepwater form was deeper-bodied and contained more fat than the lank, shallow-water form, but did not attain as large a size. Populations of trout having either of these two general body forms were recognized by fishermen at many localities throughout Lake Michigan (Goode 1884; Smith 1908). The shorter, chubbier form, taken almost invariably in deep water, was known by such local names as "pot-bellies" and "deepwater trout." The longer, slimmer form, said to be coarser-meated and usually taken in shallow water, was known as "Mackinaw," "reef-trout," and "shoal-water trout." According to Smith (1908), deepwater trout were more abundant in the southern half of Lake Michigan, where they spawned over clay bottoms in depths of 82–110 m. The Mackinaw or reef trout, on the other hand, were more abundant in the northern half of the lake, lived at depths of 11–55 m, and spawned on honeycombed rock at 11–46 m. Fragments of this rock dislodged and raised in gill nets sometimes contained lake trout eggs in surface indentations.

When considered in chronological order, the various published accounts of the fisheries of Lake Michigan suggest that populations of a fat, deep-water form of lake trout closely resembling the siscowet of Lake Superior occurred in the deeper, northern part of Lake Michigan in the 1800s but had disappeared from the catches by the 1920s. The siscowet, first described by Agassiz (1850) as *Salmo siscowet*, is still given taxonomic status as a distinct species (*Salvelinus siscowet*) by Eddy and Underhill (1974), although most other authorities assign a subspecific ranking (Hubbs and Lagler 1949) or do not differentiate it from lake trout (Scott and Crossman 1973). Because the siscowet, which is common off Isle Royal and other deep-water areas of Lake Superior, may represent the greatest degree of morphological and possibly genetic divergence from the typical lean lake trout (Eschmeyer and Phillips 1965), confirmation of the former presence of the siscowet in Lake Michigan would provide additional evidence that separate stocks of lake trout did indeed exist there.

The earliest account of the siscowet-like form of lake trout in northern Lake Michigan was given in a natural history report on the Beaver Islands area by Strang (1853), the colorful and controversial leader of a local Mormon settlement.

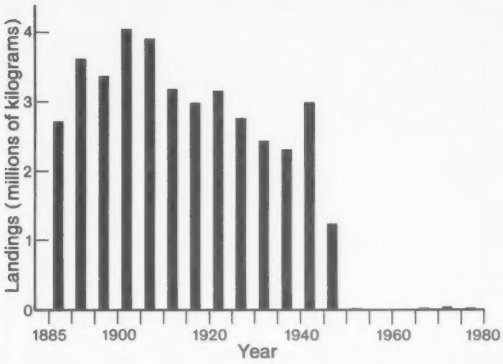

FIG. 1. Annual commercial landings of lake trout in Lake Michigan, 1885–1979 averaged by 5-yr intervals (data from Baldwin et al. 1979).

According to Strang, limited quantities of *Salmo siscowit* (sic), which he called the fattest and most valuable fish in the lakes, were taken by commercial fishermen in the Beaver Islands area, and also in neighboring Lake Huron, but those of the "best quality" were found in Lake Superior where they were very abundant in some areas. Strang also reported a white-meated trout of indifferent quality from Lake Michigan that greatly resembled the siscowet and was frequently sold under that name.

Because of the much greater value of the siscowet (and presumably similar deep-water forms of lake trout) as a salted product, compared with that of the lean reef-spawning forms, selective fishing could have contributed to their decline and eventual disappearance from the Beaver Islands region of northern Lake Michigan, as could have their incidental capture in gears fished for deep-water ciscoes (*Coregonus* spp.). In 1864, Herbert (quoted in Goode 1884), for example, described the siscowet as "the very best salt fish . . . in the world," and noted that its price per barrel in the upper Great Lakes area was more than double that of the coarser-fleshed, larger form of lake trout. True (1887) observed that the salt-fish trade around the Beaver Islands was more important than that of fresh fish. He also was informed by a local authority that overall fish abundance had declined there 40–50% since 1859.

Reports of fat forms of lake trout in northern Lake Michigan continued into the later 1800s. In the summer of 1880, Ludwig Kumlien (in Goode 1884) surveyed the fisheries in various areas and reported both fat and lean forms of lake trout on both sides of the northern (i.e. about Grand Traverse Bay and the vicinity of Two Rivers, Wisconsin) and the southern (Grand Haven, Michigan, and Waukegan, Illinois) halves of the lake. At about this time, Smith and Snell (1891) stated that the "siscowet or deepwater variety of the trout" occurred "throughout the northern portion of the lake . . . especially between the Manitou and Beaver Islands. In some places fully half the trout taken are of this kind." Perhaps some authorities questioned the extension of the known range of the siscowet beyond the confines of Lake Superior, because Smith (1894) briefly reiterated these statements 3 years later.

The status of the fat form(s) of lake trout apparently had changed markedly in northern Lake Michigan by the early 1900s. By then, Smith (1908), as noted earlier, reported that the deepwater "species" of trout was "mostly" found in the southern half of the lake. In a later report on the fisheries of the Great Lakes, Koelz (1926) stated that the lake trout in northern Lake Michigan "are shoal forms and spawn off the shore on rock bottom. There are no deepwater trout known in the north."

Nevertheless, we conclude on the basis of the persistent earlier reports of fat trout from northern Lake Michigan that a deepwater form of lake trout occurred there in the 1800s, but we have no way of determining how close this form was to the typical siscowet of Lake Superior. Milner (1874) and Goode (1884), who either were unaware of or chose not to cite Strang's article, seemed emphatic in stating that the siscowet was confined to Lake Superior. Although they later reported that the siscowet occurred in Lake Huron and even Lake Erie, Jordan and Everman (1904) made no reference to its ever having occurred in Lake Michigan; and Greene (1935) observed, after noting a Wisconsin fisherman's report of a siscowet in that lake, that its occurrence there could not be stated definitely.

Lake trout in some localities of Lake Michigan were also distinguishable by different flesh colors, ranging from white to various reddish hues. Goode (1884) noted, for example, that of two forms of trout occurring in the south end of the lake, the darker-colored one with red flesh was by far the more valuable, although some markets catering to certain European ethnic groups in later years preferred a fat trout with white flesh. Goode also reported that lake trout in Green Bay with salmon-colored flesh were called black trout by the local fishermen whereas those with white flesh were called lake trout. Flesh color in salmonids is a phenotypic effect related to diet (Saito and Regier 1970); nevertheless, broad color differences implying different food habits would suggest geographical separation of the native trout into separate stocks.

Stream-spawning stocks of lake trout, such as those of eastern Lake Superior (Loftus 1958), were not mentioned in any of the published accounts of the fisheries of Lake Michigan proper, although they are reported to have entered Kid's Creek at Traverse City in the 1800s (Price and Kelly 1976).

THE EARLY 1900S TO 1950S

Many physical (e.g. morphological) and behavioral traits reminiscent of those reported for Lake Michigan lake trout by early ichthyologists, naturalists, and raconteurs were observed by commercial fishermen who participated in the intensive lake trout fisheries from about the 1920s into the 1950s. In several series of comprehensive interviews recently conducted by investigators from the University of Wisconsin (Coberly and Horrall 1980; C. E. Coberly and R. M. Horrall unpublished manuscript), the Michigan Department of Natural Resources (W. L. Organ, G. L. Lowns, M. O. Walter, R. B. Pelletier, and D. A. Riage, Michigan Department of Natural Resources, Fisheries Division, Technical Report No. 78–7, unpublished manuscript), and U.S. Fish and Wildlife Service (C. D. Goodyear, T. A. Edsall, D. M. Dempsey, G. D. Moss, and P. E. Polański, U.S. Fish and

Wildlife Service, Great Lakes Fishery Laboratory unpublished manuscript), these former commercial fishermen described a number of phenotypes and habitat preferences of the native trout that suggest ecological adaptation into differing life forms that might be described in terms of three major groups or stock complexes.

The first group included the shallow-water reef trout, also referred to by some as lean trout or Mackinaw trout. These comparatively large trout were less deep-bodied and had lower fat content than the deepwater forms we describe later, and, as their group name implies, spawned on shallow reefs and shoals, generally at depths ranging from about 1 to 23 m and averaging roughly 12 m. We believe that these depths more accurately reflect the spawning grounds of the shallow-water trout than the greater spawning depths reported earlier by Smith (1908). The name Mackinaw was also used specifically to describe a large, white- to pink-fleshed trout within this group that spawned over honeycombed limestone outcroppings, boulders, and rubble, especially along the north shore of the lake. Other forms recognized in this group were the Beaver Island trout, a large, big-headed, white-fleshed fish that spawned on shoals and reefs in the northern island complex in State of Michigan waters; the redfin or reef trout, a large trout with white-to-pink flesh that spawned on nearshore reefs and shoals in eastern Green Bay and along the adjacent Wisconsin shoreline of the lake proper — its fin coloration possibly developing during the spawning season; the yellowfin, a fish with yellowish fins, white flesh, and large head that spawned on shallow reefs off Milwaukee; and possibly moss trout which spawned over rocky shoals covered with moss (probably *Cladophora* spp.) in Grand Traverse Bay (W. L. Organ et al. unpublished data).

Moss trout may actually be synonymous with a form of *namaycush* reported from the Charlevoix–Northport area just north of Traverse Bay called the shoal trout (Clark 1900). The shoal trout was smaller than the large Mackinaw or reef trout (Goode 1884) and spawned about a month earlier (i.e., in September) on cobble, boulder, or gravel bottom in from 0.6 to 2.4 m of water. These trout however, may represent yet another stock or stock complex, differentiated somewhat from the reef–trout complex.

The second major group or stock complex included the deepwater trout, which were generally smaller, deeper-bodied fish with a higher fat content than the shallow-water reef trout. Because of their high fat content and chubby appearance, deep-water trout were called fats or "siscowets" by the commercial fishermen in some localities; we use the term fat synonymously with deepwater in the present paper to identify this specific group of native lake trout. Deep-water trout from southern Lake Michigan spawned on predominantly clay bottom, mainly at depths of 50–85 m in a zone extending from just below Milwaukee south and then east around the lake to about St. Joseph. Deep-water trout also spawned farther north on the Sheboygan, Northeast, East, and Milwaukee reefs over clay, gravel, and limestone outcropping at depths of 55–79 m. This very extensive mid-central system of reefs was considered by many to contain the most productive spawning grounds in the entire lake. Deep-water trout that spawned there were said to be not as fat, however, as their deep-water counterparts from the southern basin. None of the (20th century) fishermen who responded to the interviewers

FIG. 2. Former lake trout spawning grounds (hatched areas) in Green Bay, off Door County, Wisconsin, including those of bay trout in the largest area on the interstate line, and reef trout in all other hatched areas. (Modified from chart 4 of Coberly and Horrall 1980.)

reported fishing for or taking the fat form of lake trout in the deep waters of the northern basin.

The third stock complex of native lake trout, consisting only of the diminutive salmon or bay trout, was found almost entirely in Green Bay and at one location in the nearby lake proper (Coberly and Horrall 1980; Smith 1933; 1937; Cook 1929). Prized as a gourmet delicacy, the small, lean, very red-fleshed bay trout produced red eggs like those of a wild brook trout and spawned about 10 days later than the much larger redfin, in deeper water over a sand, gravel, and mud substrate. Its blackish background coloration suggests the "black trout" referred to by Goode (1884). Smith (1933) recalled his father saying that bay trout were more abundant in the Green Bay locale 30 years earlier.

Over 150 different localities were described by former commercial fishermen as traditional lake trout spawning grounds (C. E. Coberly and R. M. Horrall unpublished data; W. L. Organ et al. unpublished data; C. D. Goodyear et al. unpublished data). Some areas, such as the large mid-central reef system, may have encompassed the spawning grounds of several different stocks, whereas other areas may have represented only a small section of a single stock's spawning territory — e.g. the various smaller reefs along the shores of Door County, Wisconsin (Fig. 2). The ability of many of the coop-

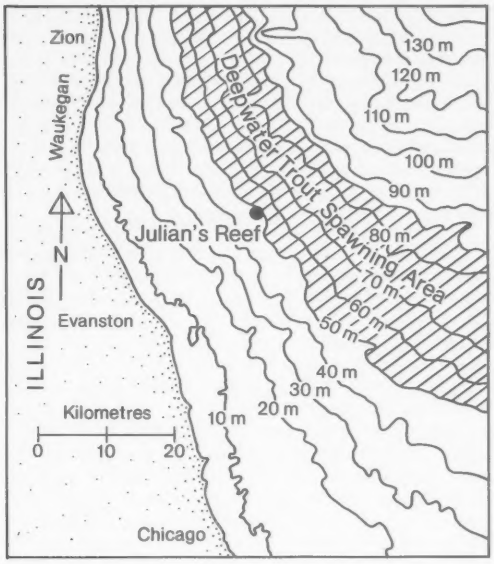

FIG. 3. Location of Julian's Reef and deep-water trout spawning ground between 50 and 85 m in Illinois waters of Lake Michigan (modified from C. E. Coberly and R. M. Horrall unpublished manuscript).

erating fishermen to recall the locations of these various spawning grounds and the "kinds" of lake trout that spawned there is attributed to the fact that for many years they had set their nets directly on the grounds in fall under permit by the states to take spawn for rearing and stocking as fry. (The stocking programs evolved over several decades because of widespread fear of overexploitation at the turn of the century; in the 1930s and 1940s, greater efforts were made than earlier to release the fry in the same areas where they were taken as spawn.)

Julian's Reef, located about 12 km southeast of Waukegan, Illinois, is one of the best examples of a physically well-defined spawning ground that was used by an apparently separate stock of lake trout distinct from the more widespread and abundant deep-water trout of the southern basin (Fig. 3). The top or shallowest part (24 m) of Julian's Reef covers several hectares of boulders and limestone outcroppings, and its sides slope downward to encompass a total area of about 259 ha. According to C. E. Coberly and R. M. Horrall (unpublished data), this reef, on which setting nets was somewhat dangerous and difficult, had been known and avoided by local fishermen since about 1900, but was rediscovered in 1939 by a fisherman who moved his fishing operation south from Washington Island, Wisconsin. The large, lean trout with reddish fins that spawned on Julian's Reef and a smaller reef to the west were reported to be similar in appearance to the redfin or reef trout found much farther north in Wisconsin waters. One fisherman interviewed by Coberly and Horrall (1980) surmised that the large trout he caught on hooks near the surface in winter in southern Wisconsin waters were the same as those taken in fall on Julian's Reef. The stomachs of some of the fish caught on hooks contained yellow perch, *Perca flavescens*, and lake herring, *Coregonus artedi*, and their body cavities had little or no visible fat, in sharp contrast to those of the deepwater trout, which foraged on chubs, *Coregonus* spp., and fourhorn sculpins, *Myoxocephalus quadricornis*. The former Washington Island fisherman reported catches up to 5200 kg per set of gill nets lifted from Julian's Reef over several years, but noted that catches were poorer there by 1945, when the spawning stock apparently had become seriously depleted. (According to other fishermen, however, sea lampreys had already preyed heavily on the stocks of reef trout in the Door County area of Lake Michigan and perhaps were beginning to deplete those in Illinois waters.)

The vulnerability to intensive exploitation and ultimately to sea lampreys of the stock of lake trout that spawned on Julian's Reef may have been typical for similar stocks of lake trout in other areas. Only the physical hardship encountered by the early fishermen because of the remoteness of such stocks may have enabled them to survive in the prelamprey period. From the fishermen's own graphic comments, one must conclude that the distance to Julian's Reef and the difficulties of fishing there kept that stock of lake trout from being depleted long before the end of World War II. Stocks of lake trout in other localities of Lake Michigan did not fare as well, judging from the concerns of the early writers mentioned above. Ironically, fishing by special permit to obtain spawn for the extensive fry stocking programs may have hastened the decline of some stocks because the trout were most vulnerable while on the spawning grounds. Van Oosten (1950), speaking for an interagency lake trout technical committee, seriously questioned whether the millions of stocked hatchery fry significantly augmented natural reproduction.

Geophysical, Temporal, and Behavioral Factors in the Development of Discrete Stocks

The inferred natural differentiation of the lake trout resource of Lake Michigan into a number of separate stocks and stock complexes is consistent with the size and varied physiography of the lake (Fig. 4) and the thousands of years since the late stages of the last glaciation during which colonization and adaptation by trout could have occurred. The final retreat of glacial ice left a vast body of water with various habitats that lake trout might exploit: large bays, island complexes, deep and thermally stable midlake basins, nearshore and offshore reefs, and substrates ranging from clay to fields of boulders and limestone outcroppings. After the glacial retreat, this large oligotrophic lake provided a relatively stable and permanent environment, not only for the trout but for coadapting populations of ciscoes (*Coregonus* spp.), sculpins (*Cottus* spp. and *Myoxocephalus thompsoni*), and other species on which the trout foraged. It also contained an abundance of macro-invertebrate food for immature trout in the form of *Pontoporeia affinis* and *Mysis relicta* (Smith 1972).

The fossil record indicates that lake trout were already present in the vicinity of Lake Michigan during the glacial shaping of its basin. Lake trout remains from a calcareous clay bed in Fenton Lake, Genesee County, Michigan, were estimated to be not more than 14 000 yr old (Wilson 1967). Lake trout skull fragments from lacustrine clay beds in the

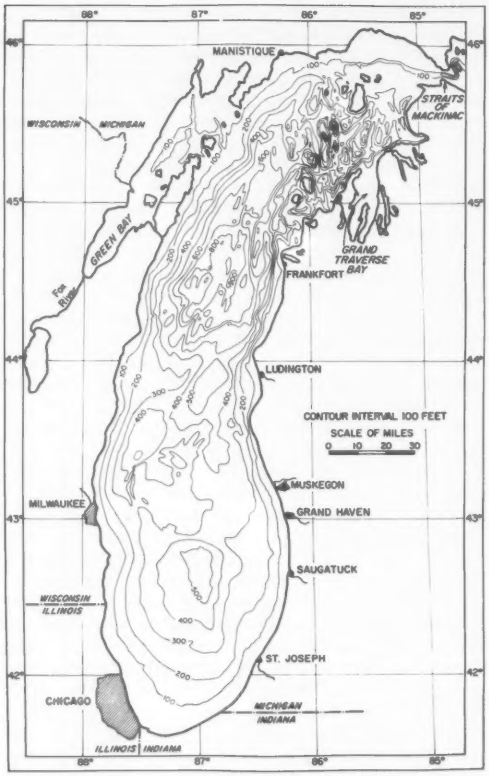

FIG. 4. Lake Michigan (modified from Hough 1958). Grand Traverse Bay, which is not contoured, has a steeply sloping bottom and a maximum depth of about 600 ft.

valley of the Red Cedar River, a tributary of the Mississippi, at Menomonie, Dunn County, Wisconsin (Hussakof 1916), were also recently assigned to the late Pleistocene (12 500–16 000 yr old) by carbon dating of surrounding deposits (Lindsey 1964).

We can only speculate, however, as to the geographic origin and the path of evolution of lake trout that colonized this large lake, presumably from a Mississippi refugium (Lindsey 1964). Did the sympatric lean and fat forms in Lakes Michigan, Huron, and Superior represent independent but parallel developments within each lake, or did they all evolve from two separate lineages each of which entered the lakes during one or more periods of water level adjustment? A recent electrophoretic study of Lake Superior stocks (Dehring et al. 1981) suggested that similar environments may have led independently in each lake to the selection and expression of similar genotypes (Savvaitova 1980). But these lakes were interconnected at least twice in the late Pleistocene, and more than one form of lake trout could have found access or egress. About 10 600 years ago, Lake Duluth, the forerunner of Lake Superior, briefly flowed by a narrow riverine connection into what is now Lake Michigan, by way of northern Green Bay. The first broad connection, however, among what are now known as the three Upper Great Lakes occurred during submersion of Michigan's Upper Peninsula about 300 years later when Lake Agassiz to the far northwest was also connected to Lake Superior by way of Lake Nipigon. The broadest and therefore possibly most important connection for the passage of fish among the three Upper Great Lakes occurred about 7500 years ago in the same general area (Bailey and Smith 1981).

Long-term fluctuations in lake water levels, between 70 and 195 m above sea level, that followed glacial advances and retreats, were probably significant factors in the evolution of various lake trout stocks described in this paper. These fluctuations were caused by the interplay of melting ice, crustal rebound, and changing seaward exits from the Great Lakes to the Atlantic Ocean or to the Gulf of Mexico. The lake's carrying capacity for this large piscivore and its prey species would have increased in periods of rising water levels, whereas falling levels would have decreased both the volume of aquatic habitat and the available spawning area. Geographic isolation of different populations would have been facilitated by falling water levels, which reached a minimum of 70 m above sea level, an estimated 8400 years ago (Bailey and Smith 1981). At that time, a smaller southern basin of then Lake Chippewa was only narrowly connected to a larger northern basin by what is called the Grand Haven River (Hough 1958). Conversely, rising water levels would have enabled formerly allopatric stocks to become sympatric and perhaps introgress.

The physical barriers that have separated spawning populations of lake trout in Lake Michigan are not as sharply defined as the separate spawning streams on the west coast of North America, which are said to circumscribe discrete stocks of Pacific salmon (Larkin 1972), and the postglacial period has provided a shorter time span for stock differentiation in the Great Lakes. Yet, from what we can determine about indigenous lake trout, similar spatial and temporal isolating mechanisms were involved in both areas. These isolating mechanisms are especially reflected in the respective shallow-water and deep-water spawning habits of the lean and fat forms of lake trout, and in the tendencies of some stocks to spawn in either early or late fall.

As noted by Ricker (1972), homing is certainly a primary reproductive isolating mechanism involved in the formation and maintenance of discrete spawning populations or stocks. This innate ability of salmonines to imprint upon and later return to their own natal streams, shoals, or reefs appears to be more highly developed in lake trout than one might expect of what is a relatively nonmigratory species (Eschmeyer 1955; Loftus 1958; Martin 1960; Swanson 1974). The basic olfactory mechanism of salmonid homing proposed by Hasler (1966) is that the home waters acquire a distinctive odor or "unique organic quality" from local soils, minerals, and plant communities — an odor that the young salmonid learns (imprints upon) and upon maturity recognizes and uses when it homes back to those waters to spawn. In Nordeng's (1977) hypothesized mechanism, on the other hand, homeward migration is an inherited (genetically programmed) response to "population-specific pheromone trails" emanating from young individuals upstream from the migrating adults. Selset

(1980) suggested that such pheromones could be "retained at the spawning site long enough to mediate homing for the particular stock" even if the fishes are absent for a period of time, citing pink salmon (*Oncorhynchus gorbuscha*) as a possible example. Lake trout might also use such cues in homing to natal reefs. The occurrence of a previously unsuspected, pheromone-mediated mechanism of spawning site selection in lake trout — a chemical signal system that may increase the probability of fish spawning at a particular site if residue of feces and sloughed mucus from previous hatches of fry is present in the substrate at that site — is suggested by preliminary laboratory experiments (Great Lakes Fishery Laboratory unpublished data). The results of these laboratory experiments, considered along with results of experimental work on Arctic char, *Salvelinus alpinus*, by Selset and Doving (1980), suggest that, with some modifications, both Hasler's and Nordeng's hypotheses could be reconciled, combined, and extended in the following general hypothesis of salmonid homing: the young fish, at some critical period before dispersal from the natal area, imprint upon a complex mixture of odors emanating from that area. Some of these odors could originate from inorganic sources such as rocks and minerals, others from the resident biota of algae, invertebrates, and fish. But for a fish stock that homes back to a particular area, the most biologically significant and distinctive cues probably would be stock-specific odors produced wholly by the fish themselves, including residual deposits of these odorant sources (feces, mucus, etc.) in the interstices of the natal substrate. Thus each discrete stock might have its own distinctive olfactory signature by which its natal waters are recognized by the fish when they return years later as homing adults.

Genetic and Environmental Influences on the Differentiation of Stocks

Within their rather narrow thermal limits (Behnke 1980), various lake trout stocks that formerly inhabited Lake Michigan were highly adapted to the lake's varied environments. Yet we are uncertain which of the differences in morphology, behavior, and life history characteristics represented genetic differences, and which represented only effects of local environmental factors such as available prey types that could influence tissue color and fatness, or the depth and temperature at which the eggs developed. According to Ricker (1972), both genetic and environmental influences have been identified with differences among native stocks of Pacific salmon (*Oncorhynchus* sp.) and steelheads or rainbow trout (*Salmo gairdneri*), but one or the other may be weak or infrequently expressed. The genetically influenced traits observed in West Coast salmonids ranged from ocean growth rates and guiding "mechanisms" in salmon to numbers of lateral line scales in steelheads and rainbow trout. Even the labile characteristic of body coloration appeared to have a genetic basis in one investigation.

Despite the dearth of comparable information on the extinct Lake Michigan stocks, laboratory and field studies on the lake trout in other U.S. and Canadian lakes have revealed or suggested possibly important genotypic differences between native populations and between certain hatchery strains, especially regarding adaptation to depth of water. Lake trout from lakes having different thermocline depths in Ontario, for example, exhibited genetically related differences in the ability to retain swim bladder gas (Ihssen and Tait 1974). Similarly, the hatchery-reared hybrids of Lake Superior lean lake trout and siscowets, which spawn at markedly different depths, were intermediate in fat content between those of their parents (Eschmeyer and Phillips 1965). Eschmeyer and Phillips also found that differences in fat content tentatively supported observations that the surviving Lake Michigan lake trout planted in the 1940s (Hacker 1957) in Green Lake, Wisconsin, were divided into two subpopulations (sample size was small, however, and the times of sampling were confounded). Some degree of genetic programming was also suggested by consistent differences in the start (time) of spawning by the Green Lake strain and eastern Lake Superior strain (lean) of lake trout under controlled hatchery conditions at the Marquette (Michigan) state fish hatchery (C. E. Coberly and R. M. Horrall unpublished data). Green Lake fish consistently spawn about 2 weeks later, making them more difficult to work into hatchery routines and scheduling. Lake trout of the Lake Superior strain may also prefer either greater depths or, more likely, lower temperatures than fish of the Clearwater (Manitoba) strain on the basis of the depth distributions of each strain during recent preliminary sampling in Lake Ontario (J. H. Elrod personal communication). Others have observed that subtle genetic differences may account for poor survival in Adirondack lakes of stocked lake trout of the Seneca Lake strain from the Finger Lakes drainage, as compared with that of zoogeographically dissimilar strains from the Adirondack uplands (Haskell et al. 1952; Plosila 1977; Webster and Flick 1975). Fish of the Seneca Lake strain have higher survival rates when planted in large, deep lakes such as Otsego and Champlain.

Despite the possibility of similar genetic expression in the native lake trout of Lake Michigan and in present introduced strains, the expression of physical and behavioral traits in lake trout may also be strongly influenced by the environment and thus be reversible or transient. (Such attributes may nevertheless have considerable diagnostic value in the delineation of stocks.) Many instances of reversible, environmentally induced changes in various attributes in salmonines and in the distantly related coregonines have been described in the literature (Hile 1937; Martin 1966; Savvaitova 1980; Todd et al. 1981). Individuals from a population of undersized lake trout, facultatively dependent on zooplankton for thousands of years in Lake Louisa, Ontario, grew larger and lived longer when transferred to Lake Opeongo, which has a forage population of ciscoes (Martin 1966). In recent laboratory tests at the Great Lakes Fishery Laboratory (unpublished data), different strains of young-of-the-year lake trout from Lake Superior (siscowets from one locality and lean trout from two localities) held in rearing tanks grew at closely similar rates for the first 6 mo on an ad libitum ration. The highly responsive growth rate would also seem to be an unreliable indicator for separating Green Lake and Lake Superior (lean) strains of lake trout in State of Michigan waters of Lake Michigan, because average lengths-at-age were similar there in the late 1960s (Rybicki and Keller 1978). Apparently a genetic component of growth, as suggested by persistent differences in growth rates of immature trout from different parents kept under the same hatchery conditions (Cook 1929), may fre-

TABLE 1. Numbers of lake trout of five strains planted in Lake Michigan in 1965–79[a]

Year planted (yearlings)	Strain					Total
	Eastern Lake Superior	Apostle Islands L. Superior	Jenny Lake Wyoming[b]	Clearwater Lake Manitoba	Green Lake Wisconsin[c]	
1965	1 275 878	—	—	—	—	1 275 878
1966	1 484 600	47 200	—	—	185 000	1 716 800
1967	2 194 976	—	—	—	229 464	2 424 440
1968	1 430 710	—	—	—	445 190	1 875 900
1969	1 760 590	—	—	—	239 215	1 999 805
1970	1 640 000	—	—	—	320 000	1 960 000
1971	2 128 145	—	—	—	215 400	2 343 545
1972	2 668 880	—	—	—	256 640	2 925 520
1973	2 110 450	—	—	—	389 700	2 509 150
1974	1 397 100	—	—	260 250	740 000	2 397 350
1975	1 305 374	—	—	200 050	1 072 000	2 577 424
1976	1 694 500	—	—	—	853 300	2 547 800
1977	2 320 100	—	—	47 500	—	2 367 600
1978	2 589 400	—	—	—	—	2 589 400
1979	2 439 026	—	4171	13 900	—	2 547 097
Total	28 439 729	47 200	4171	521 700	4 954 909	33 967 709
Percent	83.7	0.1	0.0001	1.5	14.6	100

[a]Data provided by Great Lakes Fishery Commission.
[b]Descended from lake trout of multiple geographic origins — Federal Fish Hatcheries of Northville (Michigan) and Bozeman (Montana); and Manitoba.
[c]Descended mainly from native Lake Michigan fish hatched in facilities of the State of Wisconsin at Sturgeon Bay or Sheboygan (Hacker 1957).

quently be masked by environmental conditions. Yet strong experimental evidence has shown a substantially faster growth rate for young lake trout of the Seneca Lake strain than for two strains from the Adirondacks region when the fish are reared under similar conditions (Haskell 1952).

Efforts to Regain Reproductively Viable Stocks

The massive stocking program in Lake Michigan, aimed since its inception in 1965 at restoring self-sustaining populations and regaining some degree of the productivity formerly represented in native stocks, has included five strains of lake trout: (1) an eastern Lake Superior strain, stocked mostly in the northern two-thirds of the lake, composing the largest number of fish planted over the years; (2) an Apostle Islands strain from western Lake Superior, released at only two sites along the north shore in 1966; (3) a Clearwater Lake, Manitoba strain, stocked at scattered locations in the 1970s; (4) a Green Lake, Wisconsin strain, planted mostly in the southern one-third of the lake and descended mainly from fish that were native to Lake Michigan; and (5) a Jenny Lake, Wyoming strain, planted in Wisconsin waters of the lake at McKinley Park in 1979 and descended from hatchery-reared fish from Federal Fish Hatcheries of Northville (Michigan) and Bozeman (Montana), and from Manitoba (Table 1).

Since the mid-1970s, up to 50% of all lake trout planted each year have been released offshore by car ferry and other means — some on reefs where native fish were known to have spawned in the prelamprey period. This more difficult and costly procedure is intended to counteract the strong tendency of shore-planted lake trout to return as adults to the areas where they were planted, which are often unsuitable for spawning (Pycha 1973; Lawrie and Rahrer 1973).

In spring 1976, 277 000 yearlings of the Green Lake strain were planted in a special experiment on the deep, midlake Sheboygan Reef, where some of their native forebears were known to have spawned (Smith 1908; Hacker 1957). Many trout from that planting were present on the reef as subadults during monitoring from a research vessel in September 1979 (Great Lakes Fishery Laboratory unpublished data). Until they are sexually mature, however, it will not be known whether significant numbers of this sole surviving strain of Lake Michigan lineage will spawn on the reef instead of migrating far inshore to spawn, because of possible imprinting or conditioning to shallow depths in the hatchery.

Many fish of the various hatchery strains have congregated in spawning condition at locations along the shoreline each year since 1970, and more recently on several offshore reefs. Yet the only conclusive evidence that they have reproduced successfully was the collection of eyed eggs and fry on intake screens of a power plant and on nearby rock structures in the west arm of Grand Traverse Bay in 1976–79 (Wagner 1980), and of fry and fingerlings in trawls near the James Campbell Power Plant, south of Grand Haven, Michigan, in 1980 (David J. Jude personal communication). According to records of planting locations, these naturally produced fry in Traverse Bay and near Grand Haven may have been from parents of the Lake Superior and Green Lake strains, respectively (Great Lakes Fishery Commission unpublished data). The fry in Grand Traverse Bay are believed to have hatched near the power plant water intake, on rock structures forming protective substrate similar to that which apparently had shielded fry discovered at a power plant intake at Marquette Harbor, Michigan, in Lake Superior in 1975. The

TABLE 2. Number (thousands) and mean weight (g) of yearling lake trout of the 1966 through 1973 year-classes stocked at six locations in southeastern Lake Michigan, and catch per unit of effort (CPE: number caught at age VI per 305 m of graded-mesh gill net) off Saugatuck, Michigan, 1971–77.

	Year-class							
Stocking site	1966	1967	1968[a]	1969	1970	1971	1972	1973
Montague	—	—	69	—	75	50	50	49
Grand Haven	—	—	—	—	—	—	—	50
Port Sheldon	165	141	64	135	—	26	—	—
Saugatuck	—	—	—	—	75	—	60	—
South Haven	—	—	—	—	75	50	60	50
Benton Harbor	—	—	—	—	75	49	60	49
Total	165	141	133	135	300	175	230	198
Mean weight	25.5	16.5	23.0	20.9	16.3	16.5	21.9	17.0
Age VI CPE[b]	4.86	3.63	0.55	4.71	1.74	0.95	3.38	1.75

[a]Excluded from correlation analysis because of unexplained discrepancy in CPE at age VI relative to that at age VII.
[b]Adjusted to a standard stocking rate of 100 000 fish per year for comparison of relative survival to age VI.

presence of small percentages of older lake trout without clipped fins among those sampled from research vessels in recent years may also indicate limited natural reproduction (all hatchery trout have been finclipped before planting), but the rarity of young trout without these distinctive marks strongly suggests that fin regeneration may have occurred among older fish bearing a full complement of fins.

Comparison of Population Characteristics of Native and Introduced Lake Trout

Despite the probable loss by the early 1900s of some stocks that were easily accessible to fishing, the well-adapted stocks and stock complexes that we infer composed the prelamprey lake trout resource of Lake Michigan were still productive until almost the end of World War II. Conservative inferences about the survival, growth, and exploitation rates of that period, coupled with recorded catch statistics, suggest that roughly 8 million yearlings were produced each year during 1927–44 (Great Lakes Fishery Laboratory unpublished data), when the harvest averaged 2600 t. This high natural production far overshadows the average stocking rate since 1965 of 2.3 million young per year — fish which, unlike the wild trout of the past, must acclimate, disperse, and generally adjust to an unfamiliar lake environment.

At face value, the numbers and biomasses of the hatchery-reared fish that have survived to adulthood would seem more than adequate to produce numerous, easily detectable progeny. However, the most comprehensive recent analyses, based on an estimated survival rate of 52%, the age-specific mean weights of individual fish, and the numbers of trout in each year-class stocked since 1965, placed the 1979 standing stocks in all jurisdictions combined at a conservative 2.5 million fish weighing 1600 t (Great Lakes Fishery Laboratory unpublished data). Judging from this estimate, the present standing stock is only a small fraction of that which sustained the stable commercial yields in 1927–44. Indeed, a fishable biomass of 8700 t would have been required in 1927–44 for a hypothetical (but reasonable) exploitation rate of, say, 0.3 to yield the 2600 t that were actually reported.

Inferences about the present size of the standing stock, as suggested by the estimate for 1979, should be qualified in several respects. The 52% survival rate used in the calculations (Great Lakes Fishery Laboratory unpublished data) is a weighted value based on that for age-VI and older adults sampled off Saugatuck, Michigan (Great Lakes Fishery Laboratory unpublished data), with graded-mesh gill nets in fall 1976–78 (52%) and the average for 2- and 3-yr-old immature trout sampled in trawls off Grand Haven, Michigan (Great Lakes Fishery Laboratory unpublished data), during 1972–74 (43%) and in Good Harbor Bay, Michigan (Rybicki and Keller 1978), during 1973 through 1976 (63%). Any serious error in the overall survival rate would most likely be associated with that estimated for immature trout, which are difficult if not impossible to sample accurately with standard gear during and after their dispersal from planting sites. Use of the survival method to estimate the standing stock consequently involved the unrealistic assumption that unknown poststocking mortality is the same for each year-class.

Evidence for dramatic differences in poststocking mortality was recently provided by analyses of year-class success from the time(s) of stocking to full recruitment to the adult stock at age IV, when the trout were sampled with graded-mesh gill nets near Saugatuck in 1972–79 (Great Lakes Fishery Laboratory unpublished data). The 1966 year-class, for example, was five times better represented at age VI than was the 1971 year-class at the same age after the numbers of age-VI fish caught per unit of effort (CPE) were adjusted to account for different stocking densities at six sites along a line extending 80 km north and south of Saugatuck (Table 2). That such differences in year-class strength may have been established very early is supported by a strong correlation between abundance at age VI and mean weight at planting ($r = 0.78$, 5 df). The larger yearlings may have been better able to avoid predators, to adapt to a competitive lake environment, to overwinter, and in general to withstand the many stresses (e.g. temperature change) associated with stocking than were the smaller fish. Their large size resulted from longer retention in the hatchery in spring (April–May) when almost all of Lake Michigan's piscivorous fish species are concentrated in the warmer nearshore waters and predation is most severe.

Although techniques for measuring poststocking mortality are obviously needed to improve future estimates of stock size, management should be even more concerned about the numbers of planted trout that now survive to maturity and contribute for a sufficient span of years to the population's

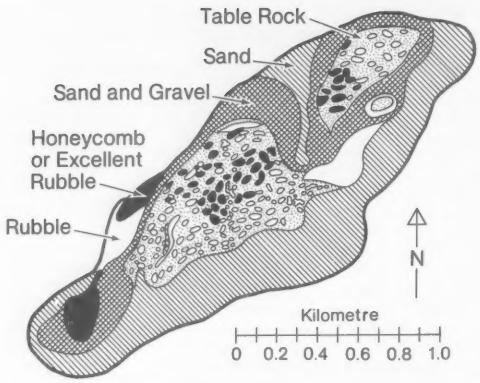

FIG. 5. Types of bottom material overlying Horseshoe Reef in Green Bay of Lake Michigan, as determined from underwater observations by divers (modified from Stamm et al. 1979).

reproductive potential. A large spawning population is indeed essential if the present stocked fish are possibly deficient in heritable adaptive traits possessed by native fish. Another important factor with respect to the apparent inability of planted fish to reproduce themselves is the severance by extinction of the long physiological–behavioral "thread" that enabled native fish to imprint upon and later relocate and spawn over favorable habitat. Presumably through the mechanism of site imprinting, the well-adapted and widespread native lake trout were able to find and spawn on the more suitable areas where they were produced. Today's planted lake trout appear to be using some of the same traditional spawning reefs and shoals in Lake Michigan (Peck 1979), but these areas contain many different types of substrate, only a small fraction of which may be suitable for the protection and incubation of lake trout eggs and fry (Fig. 5). Because planted trout have probably not received the requisite cues essential for site imprinting, they may distribute their eggs independent of subtle but perhaps extremely important differences in substrate type. Whether fertilized eggs are deposited in sufficient numbers on the best areas of a particular reef or shoal to overcome environmental resistance to reproduction (i.e. predation on eggs and fry as well as all other sources of mortality) may now be due largely to chance and thus related directly to the number of spawning fish in the vicinity of that specific site. As explained earlier, however, the size of the present lake trout spawning stock in Lake Michigan is comparatively small — perhaps so small that it may be unable to overcome the suspected reproductive inefficiency of the planted fish.

Conclusions and Recommendations

From our point of view, the main rationale of the stock concept is to prevent the dilution or loss of the gene pools of native fish populations, the adaptive norms of which are closely keyed to their respective environments. Because past environmental changes have influenced the present degree of genetic variability in various adaptive characters, each population now has a defense against recurrent change in local environmental conditions. Therefore, to avoid reductions in fitness that could in turn result in disastrous reductions in production, the genetic integrity of natural fish populations should be preserved. The validity of these tenets may be reflected in some of the difficulty now being experienced in the continuing effort to reestablish self-sustaining lake trout populations in Lake Michigan following the extinction of the diverse native stocks.

As we noted earlier, the continuing 15-yr program to reestablish self-sustaining lake trout stocks in Lake Michigan has been built around massive annual plantings of hatchery-produced yearlings principally from two distinct strains, the Green Lake strain and the eastern Lake Superior strain. With expectations that they have retained heritable traits of adaptive value, the Green Lake fish have been stocked primarily in the southern third of Lake Michigan where some of their progenitors are believed to have originated. Likewise, the eastern Lake Superior fish have been stocked primarily in the northern two-thirds of Lake Michigan, an area to which they too should be well adapted because of its geographical proximity to their native latitudes and because of an abundance of similar shallow-water spawning habitat. Although both tactics appear to be generally sound, hindsight has nevertheless suggested errors that may be blocking attainment of the goal of self-sustainability. To prevent, what appears to be, the most serious of these errors from reoccurring, we recommend the following changes in the lake trout planting program:

1) Ensure that future plants of lake trout in Lake Michigan possess as many of the genetic complements of wild stocks as possible. This could be accomplished by routinely obtaining eggs from wild stocks in the field, thus making the holding of brood stock in hatcheries unnecessary; by maintaining hatchery brood stocks derived from wild fish and replenishing a certain proportion each year from the same wild stocks; or by holding only females from wild stocks and collecting sperm from their respective wild populations. Risks of additional disease problems in hatcheries using these procedures could perhaps be minimized by the development of appropriate prophylactic methods.

2) As in the past, consider using progeny from remnant stocks of wild Lake Superior lake trout for recolonizing Lake Michigan, including siscowets as well as the lean form which has been the mainstay of the planting program to date. Following the glacial retreat, Lakes Michigan and Superior were possibly colonized by lake trout in a south-to-north direction. Surviving Lake Superior stocks may therefore retain enough of the original genetic plasticity needed to readapt to Lake Michigan's various environments. Other native stocks of fish originally derived from prelamprey populations of Lake Michigan lake trout may also survive in small tributary lakes, particularly Torch Lake near Grand Traverse Bay (M. Keller personal communication). Each form of wild trout, whether selected from Lake Superior or from lakes such as Torch, should be carefully planted in habitat similar to that from which they are removed (i.e. type and depth of spawning substrate).

3) Supplement our recommended use of broodstock from extant wild stocks in the Great Lakes by continuing to obtain progeny from trout of the Green Lake strain for stocking in carefully selected areas. Outcrosses of these descendants of native Lake Michigan lake trout should be discouraged. In-

stead the genetic makeup of this strain, now being held at Crystal Springs Hatchery, Wisconsin, could perhaps best be strengthened by an infusion of genes from feral fish of the 1976 plant on the Sheboygan Reef, especially if these fish demonstrate the desired behavioral trait of remaining and spawning on the mid-lake reef complex. However, plants of the Green Lake strain need not be limited to deep-water spawning grounds. Chances are good that part of the Green Lake strain's native complement of genes was derived from a shallow-water form of lake trout that spawned north of Sturgeon Bay, Wisconsin, and that another part originated from the deep-water form. These northern shoal areas should therefore also be seriously considered as suitable planting locations for fish of the Green Lake strain in the future.

4) Because improvement in genetic fitness alone will not guarantee future self-sustaining populations of lake trout in Lake Michigan, allow the planted fish to survive to advanced ages of higher fecundity in sufficient numbers to overcome their suspected inability to deposit eggs over suitable substrates and depths. The question of genetic fitness as a factor limiting successful reproduction may even be of secondary importance and partly irrelevant in solving the rehabilitation riddle. But unfortunately, no one knows the numbers of feral adults that would be necessary to produce significant numbers of young on specific Lake Michigan spawning grounds. Even the estimated densities of native spawners on Lake Superior reefs may be misleading by comparison, because those fish are presumably well adapted to local environments there, and may be reproductively efficient.

5) Finally, in addition to greatly reducing exploitation of the planted lake trout, it should be determined whether higher planting densities than those used since 1965 are necessary to overcome the suspected reproductive inefficiency of the hatchery-reared trout. Lake trout that reproduced successfully in two Ontario lakes were stocked at the rates of 5.3 (Olver and Lewis 1977) and 12.0 (Purych 1980) yearlings per hectare as compared to an average rate of 0.41 yearlings per hectare in Michigan.

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Life History and Timing of Migrations and Spawning Behavior of Rainbow Trout (*Salmo gairdneri*) Populations of the Great Lakes[1]

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Rainbow trout (*Salmo gairdneri*) populations of the Great Lakes showed a great variability in timing of spawning migrations and life histories. This variability was examined to determine if rainbow trout populations of the Great Lakes are comprised of discrete stocks. Differences in timing of migration and spawning indicated that at least one spawning population may be distinctive and that others may be in progressive stages towards emergence of discrete stocks. The innate ability of this species to adapt to different environmental conditions, together with its ability to 'home,' provide rainbow trout in the Great Lakes with the potential to develop discrete stocks. The management of this species that allows for the development of this potential is emphasized.

Key words: rainbow trout, Great Lakes, stocks, migrations, spawning, life histories, homing

BIETTE, R. M., D. P. DODGE, R. L. HASSINGER, AND T. M. STAUFFER. 1981. Life history and timing of migrations and spawning behavior of rainbow trout (*Salmo gairdneri*) populations of the Great Lakes. Can. J. Fish. Aquat. Sci. 38: 1759–1771.

Il existe parmi les populations de truites arc-en-ciel (*Salmo gairdneri*) des Grands Lacs une grande variabilité du calendrier des migrations de ponte et du cycle biologique. Nous avons examiné cette variabilité afin de déterminer si les populations de truites des Grands Lacs sont formées de stocks séparés. Les différences de temps de migration et de ponte indiquent qu'au moins une population reproductrice pourrait être distinctive et que les autres seraient à divers stades d'évolution vers des stocks séparés. La truite arc-en-ciel des Grands Lacs, avec son aptitude innée à s'adapter à différentes conditions ambiantes, couplée à celle qu'elle a de retourner à sa rivière natale, a le potentiel de former des stocks séparés. Nous mettons en vedette une gestion de l'espèce qui favoriserait la réalisation de ce potentiel.

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ALTHOUGH native to the west coast of North America, rainbow trout (*Salmo gairdneri*) have been introduced to many waters of the world including the Great Lakes Basin (MacCrimmon 1971). Since 1874, introductions of various life stages of this species from many parts of its native range have produced self-sustaining populations in all five Great Lakes (MacCrimmon and Gots 1972). In this paper we examine rainbow trout populations that enter tributaries to the Great Lakes and attempt to determine if this species has adapted sufficiently to the catchment to have developed distinctive "stocks." The definition of "stock" is fashioned after Ricker (1972), "... fish spawning in a particular lake or stream (or portion of it) at a particular season, which fish to substantial degree do not interbreed with any group at a different season ...".

Many forms of rainbow trout have been introduced to the Great Lakes. The details of this history are complex; further information is available in MacCrimmon (1971) and MacCrimmon and Gots (1972). Self-sustaining rainbow trout populations in the Great Lakes are usually anadromous, migrating upstream in spring and autumn as maturing adults. Spawning occurs usually in spring, but some autumn–winter spawning has been observed (Dodge and MacCrimmon 1971; Gordon 1978). Juveniles spend 1–3 years in the parent

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TABLE 1. Location and physical characteristics of the tributaries used to study the vital statistics of rainbow trout spawning populations of the Great Lakes.

Tributary	Lake	Province/ State	Lat. N	Long. W	Drainage area, ha	Stream length, km	Stream gradient, m/km
Ganaraska	Ontario	Ontario	43°56′	78°18′	27 994	42	5
Big Creek	Erie	"	42°36′	80°27′	72 397	97	1
Lucknow	Huron	"	43°51′	81°38′	23 089	45	3
Colpoys	"	"	44°47′	81°07′	906	4	10
Pottawatomi	"	"	44°34′	80°56′	9 918	18	14
Sydenham	"	"	44°31′	80°56′	18 130	37	35
Telfers (Bothwells)	"	"	44°37′	80°53′	5 823	32	10
Silver	"	"	44°31′	80°16′	2 077	25	21
Nottawasaga	"	"	44°30′	80°01′	409 858	135	2
AuGres	"	Michigan	44°05′	83°40′	32 500	200	
Stokely	Superior	Ontario	46°49′	84°24′	6 000	13	17
Batchawana Bay[a]	"	Ontario	46°50′	84°30′			
McIntyre	"	Ontario	48°25′	89°16′	15 410	63	4
Kadunce/Kimball[b]	"	Minnesota	47°50′	90°01′	3 880	11	20
Huron	"	Michigan	46°55′	88°05′	20 000	60	
Black	Michigan	"	46°05′	85°20′	7 290	50	
Platte	Michigan	"	44°45′	86°10′	36 000	70	
Little Manistee	Michigan	"	44°15′	86°15′	50 000	200	

[a]Includes several tributaries to Batchawana Bay.
[b]Includes the two similar tributaries Kadunce and Kimball creeks.

stream, then migrate to the Great Lakes where they grow rapidly to maturity. However, rainbow trout populations exhibit variability in life history patterns and spawning migrations. We intend to analyze this variability as a means of distinguishing stocks. In this paper we describe timing of spawning runs, duration of spawning, homing and straying, life histories of adults in the spawning runs, and life histories of juveniles in nursery streams. Rainbow trout in open waters of the Great Lakes are not discussed.

Materials and Methods

Information on the timing of spawning and adult migrations resulted from interviews[2] of 75 fisheries management staff and rainbow trout anglers who were familiar with rainbow trout streams on the Great Lakes as well as from examination of various reports and theses about Great Lakes tributaries. Data on homing and the life histories of rainbow trout populations were taken from a variety of publications and theses dating from 1932 to 1980. Only those adult rainbow trout populations with life history data on 100 or more fish from 18 individual tributaries were selected for study. The exceptions were for Batchawana Bay and Kadunce and Kimball Creeks, where data were lumped for spawning populations from several tributaries to Batchawana Bay, a small bay on the east coast of Lake Superior; data from Kadunce and Kimball Creeks, two small adjacent Minnesota tributaries to Lake Superior, were combined and will be referred to subsequently as Kadunce/Kimball Creek.

The 18 study streams included tributaries to all five Great Lakes (Table 1). Eight streams drain to Lake Huron, five to Lake Superior, three to Lake Michigan, and one each to Lake Ontario and Lake Erie. Catchment size varies from less than 1000 to over 400000 ha. The shortest stream is Colpoys Creek (4 km) and the longest are Little Manistee River and AuGres River at 200 km. The gradients are also variable ranging from relatively flat at 1 m/km to steep at 35 m/km (Table 1).

Flow characteristics of all streams are similar and typical of streams to the Great Lakes. Discharges are extremely low during July and August owing to low precipitation and again in January and February because of freezing conditions. Peak water flow occurs in March and April when precipitation is high and ice and snow are melting. Frequently heavy April rains add to spring freshets. A lesser peak usually occurs in October and November during autumn rains.

Although the life histories data used in this study were obtained from a variety of independent studies, the methods used to collect the data were similar (Table 2). At selected locations on the study streams spawning populations were sampled on their upstream migration with either a weir, fishway, or electrical barrier. In some cases an electrofisher and dip net were also used. Some creel census data were included. Sampling was done on a set schedule each spring and frequently each autumn. In most cases subsamples of the entire run of rainbow trout were measured, sexed, and examined for maturity. In others, sampling was done as closely as possible to the peak of migration, providing samples representative of the bulk of the spawning fish.

Scale samples were collected for aging. Scales were examined to determine years of stream life, years of lake life, or total age. In a few cases, age at first spawning and total spawnings were determined from spawning checks. Criteria and recording methods were adapted from Shapovalov and Taft (1954), by Dodge (1967).

The sampling periods varied considerably both between and within streams (Table 2). The earliest period was 1928

[2]A copy of the 14-page interview record form is available from the authors on request.

on the Little Manistee River and the latest was 1979 on the Lucknow and Ganaraska rivers. The longest continuous sampling period was 17 years from 1961 to 1977 on the Nottawasaga River and the shortest was 1 year (1978) on Colpoys Creek. However, most of the populations of the streams were sampled during 1966–80. Additional information on the description of the study streams and on the methods used to collect the data can be obtained from the source material listed in Table 2.

Results and Discussion

Timing of Migration and Spawning

Usual migration time — Winter–spring migrations by maturing adults into ~ 300 tributaries throughout the Great Lakes began as early as January or as late as the 1st week in May. However, migrations for most (except Lake Superior) started during the first half of March, whereas fish entered Lake Superior tributaries initially in the 1st week in April. Timing of peaks varied, usually occurring 2–4 weeks after runs began. Adults sometimes continued to enter Lake Erie tributaries as late as June and early July. The mean duration of the spawning migrations ranged between 4 (Lake Superior) and 7.5 weeks (Georgian Bay) of Lake Huron. The anomalies in these patterns will be described below.

Approximately half the Great Lakes tributaries with spring migrations also have autumn runs. For autumn runs, fish enter streams in the 1st week of September, and continue to run sporadically to the end of December. Most autumn migrations were completed between 4 and 8 weeks. Observers suspected that fish in most of these autumn migrations laid over winter or returned to the lake to migrate once again the following spring. Winter (1976) reported for rainbow trout in Minnesota tributaries to Lake Superior that ripe animals of both sexes were encountered, but he speculated that fall–winter spawning was probably rare. Instead he believed that fall-run fish overwintered to spawn with spring migrants. Further, Winter believed that autumn storms formed large gravel bars along river mouths and prevented significant numbers of autumn migrants from ascending many Lake Superior tributaries.

Usual spawning time — For 11 tributaries to Lake Ontario, observed winter–spring spawning started as early as the 1st week in March and as late as the 4th week in April, although spawning had begun by the 1st week in April in most streams. Spawning continued in some streams to as late as the 2nd week in May, although fish in five streams had completed spawning by the 4th week April. The duration of spawning activity was short ($\bar{x}$ = 3.0 weeks), although fish in one stream spawned over 6 weeks and some in another for 9; in both of these streams, adults had started spawning by the 2nd week in March.

Winter–spring spawning observed in six streams tributary to Lake Erie started in either the 1st or 2nd week of April, finishing anytime between the 4th week in April and the 4th week in June. The duration of spawning activity averaged 6 weeks, varying between 2 and 11.

Fish in 13 streams on Lake Huron started spawning in April (the earliest was the 1st week) and the latest began during the 2nd week of May. Most fish completed spawning between the 4th week of April and the 2nd week of May, although one run of fish continued spawning until the 2nd week of June. Spawning activity continued for an average of 3.7 weeks, ranging between 1 and 9.

Spawning activity in most (19 of 24) tributaries to Georgian Bay of Lake Huron started in April, but in some streams fish started to spawn in March, in one during the 2nd week in February, and in another in the 1st week in January. Fish in most streams completed spawning between the 4th week in April and the 3rd week in May; however, in one stream, fish continued to spawn until the 1st week in June. Sixty-three percent of the fish completed spawning in 4 weeks or less, another 26 percent in 9 weeks, and in two more streams in 13 and 17 weeks each. The average duration of spawning was 6.2 weeks. Extensive information was available on the pattern of these activities for fish in three tributaries (Pottawatomi River, Sydenham River, and Telfers Creek) and will be discussed below.

In tributaries to Lake Superior spawning started between the 4th week of April and the 3rd week of May, and finished before the 2nd week of June. Occasional spawning was observed as late as July.

Anomalies — Atypical migration and spawning behavior occurred in six tributaries to Georgian Bay of Lake Huron and one tributary to each of Lake Erie, Lake Superior, and Lake Michigan. Rainbow trout in three Georgian Bay tributaries, Pottawatomi and Sydenham rivers, and Telfers Creek were studied between 1965 and 1970 by Dodge (1972). In each stream, excepting the 1968–69 spawning season when the winter run was absent, three distinct migrations of trout occurred, one between the 2nd week of November and the 2nd week of December, another between the 4th week of January and the 1st week of March, and the last between the 4th week of March and the 2nd week of April.

Between the 2nd week in November and the 2nd week in March, prespawners in the Pottawatomi and Sydenham rivers remained in the lower reaches of each stream, whereas, by the 2nd week in December, fish in Telfers Creek ascended to headwaters and small spring-fed tributaries.

First spawning in these three Georgian Bay tributaries varied widely. The earliest recorded spawning was in Telfers Creek immediately following the completion of the autumn migration. Spawning began during the 4th week of December and continued throughout the next 5 months to finish in late May or early June. Eggs collected from nests prepared by the December spawners were reared to successful hatching in an instream incubator (Dodge 1967).

Increases in the intensity of spawning followed closely after the peaks of the later winter and spring runs. In the Pottawatomi River, spawning first began following the winter migration, never immediately after the autumn movement. In the Sydenham River, no spawning began until the 1st and 2nd week in April, following the spring migration. Maturing fish that entered the Pottawatomi River in the autumn pulse and the Sydenham River in the autumn and winter pulses could not migrate to headwaters because of dams and falls. In Telfers Creek, however, there were no obstacles to upstream migration once the autumn freshet occurred, so rainbow trout ascended immediately to warmer headwaters (3–4°C) from the cooler Owen Sound and lower reaches of the stream.

TABLE 2. The sampling dates and methods used to sample the spawning populations of the study tributaries to the Great Lakes.

Tributary	Sampling period																					
	1928	1929	1930	1942	1950	1952	1954	1956	1958	1960	1962	1964
Little Manistee	x	x (97)	x									
Platte				x (477)								
AuGres				x (120)		x	x (850)					
Black					x	x	x (537)	x	x			
Silver									x (181)	x		
Kadunce/Kimball										x	x (494)	x	x	x	x
Nottawasaga										x	x (2033)	x	x	x	x
Telfers (Bothwells)															x
Pottawatomi															
Sydenham															
Big Creek															
Huron															
Batchawana Bay															
Stokely															
Ganaraska															
McIntyre															
Colpoys															
Lucknow															

[a]On the tributaries where the sampling period has been subdivided, the sample size for each subperiod is shown separately.

Rainbow trout in three other Georgian Bay tributaries, Bighead and Beaver rivers and Indian Brook, had three distinct adult migrations similar to those in the Pottawatomi and Sydenham rivers and Telfers Creek. F. Marshall (Ontario Ministry of Natural Resources, Owen Sound District Office, Owen Sound, Ont. 1980, personal communication) observed winter spawning in the Bighead River only during the 4th week in December; these results coincided with the winter spawning dates for fish in Telfers Creek. The adults that migrated during autumn and winter into the Beaver River apparently remained in lower reaches to spawn with spring migrants during March and April. The success of the December spawning in the Bighead River is unknown. Although no measures of hatching are available, Marshall stated that the winter spawning in the Bighead River was a common occurrence.

There are some other similarities between these two groups of streams. Firstly, the Bighead and Beaver rivers and Indian Brook are close geographically, stream mouths within a 9-km range, and the Pottawatomi and Sydenham rivers and Telfers Creek are within 6 km of each other. Secondly, as in Telfers Creek, fish in the Bighead River can ascend unimpeded to the headwaters and feeder streams during the autumn migration; once there winter spawning occurs as it did in Telfers Creek. Autumn runs into the Beaver River historically were thwarted by a dam only several hundred meters upstream from Georgian Bay until a fish pass operated first in 1980 opened the way to the upper reaches. It is possible that when autumn-run fish are able to reach these upper reaches, then winter spawning may occur in the Beaver River also.

In Normandale Creek, a tributary to Lake Erie, Gordon (1978) reported that adult fish entered the stream from October to May, following freshets. Three periods of spawning activity were identified; in the 2nd week of November, January, and April. Most of the activity occurred during April. In addition, A. Elsey (Ontario Ministry of Natural Resources, North Central Regional Office, Thunder Bay, Ont. 1980, personal communication) reported that rainbow trout ascend the MacKenzie River, a tributary to Lake Superior, in two waves, an autumn run between the 2nd week

The source of the vital statistics data used in this paper is also shown. The sample size for each period is shown in parenthesis.[a]

1966	1968	1970	1972	1974	1976	1978	1980	Sampling method	Source
	x x x x (453)				x x (2451)	x		Weir	Greeley 1933; Mich. Dep. Nat. Res.
	x x x x (868)								Reynolds 1947; Mich. Dep. Nat. Res.
								Weir	Shetter 1965
								Weir	Mich. Dep. Nat. Res.
								Weir	Lamsa 1963
								Weir	Hassinger et al. 1974
x x x x x (1282)			x x x x x x x (1379)					Fishway	Wainio et al. 1972 Ont. Min. Nat. Res.
x x x x x (1596)								Weir	Dodge and MacCrimmon 1970
								Electro-fisher dip net	Dodge 1972
x x x x x (752)								Weir Electro-fisher Dip net	Dodge 1972
x x x x x (496)								Fishway Dip net	Dodge 1972
x x x x x (811)			x x x x (202)					Fishway electro-fishing	Ont. Min. Nat. Res.
x x (288)								Electri-cal barrier	Miller 1974
x x x x (461)								Weir (1970) Creel and commercial catch	Kwain 1971
		x	x x x	x x (852)				Weir	Kwain (In press)
				x x	x x (11 668)	x x	x	Fishway	Ont. Min. Nat. Res.
				x x (193)	x			Weir and fishway	Ont. Min. Nat. Res.
						x (102)		Weir	Ont. Min. Nat. Res. Grieve 1979
						x x (1318)	x	Fishway	Ont. Min. Nat. Res.

in October and the 3rd week in November, and a spring run between the 4th week in April and the 4th week in May. No winter migrations have been observed. Subsequently, fish spawned during the 2nd and 3rd weeks in October and during May, after autumn and spring runs, respectively. No measure has been made of the success of the early October spawning, although Elsey indicated that this phenomenon occurred regularly each year.

Atypical maturing and spawning behavior of rainbow trout was observed in the late 1960s and early 1970s in Lake Michigan and Platte River. In Lake Michigan, running-ripe females were taken by survey gear or anglers during most months from May through January (M. Keller, Michigan Department of Natural Resources, Charlevoix Great Lakes Station, Michigan 1980, personal communication) and spawning was observed (J. Spencer, Angler, Traverse City, Michigan 1980, personal communication). Several males and females were seen spawning in late May–early June in water less than 1 m deep over a gravel bottom next to shore. In Platte River, Taube (1974) reported that the incidence of ripeness of rainbow trout migrating upstream increased from 0 (Oct. 16) to 22% (Nov. 23). Subsequently, Taube observed several redds in late fall. Winter (1976) reported also that ripe male and female steelhead trout have been encountered frequently in Lake Michigan, and both sexes observed on redds in the Platte River, Lake Michigan, during autumn. Finally, Winter suggested that the many introductions into Lake Superior of "fall-spawning" strains of steelhead rainbow trout may have created a potential for not only fall migrations but also for autumn–winter spawning to occur.

Homing and Straying

On the basis of recaptures of marked trout to the site of initial marking, rainbow trout populations of the Great Lakes tended to return to streams of previous spawning experience and consequently 'home.' Dodge (1972) reported that 96–98% of the 304 recoveries of marked adult trout occurred in or within 8 km of the three streams of initial marking — Telfers Creek, Pottawatomi River, and Sydenham River, trib-

utaries to Owen Sound of Lake Huron. Straying into adjacent streams ranged from 3 to 10%. Three trout were taken 64 km from the initial capture and one recovery was 72 km from the initial capture. Dodge suggested important distinctions among the fish in the three streams tributary to Owen Sound. Although tagged adults from Telfers Creek were commonly recaptured in subsequent spawning migrations to the Sydenham and Pottawatomi rivers, no marked rainbow trout from the latter rivers were taken in Telfers Creek. Angler recoveries of tagged fish from Owen Sound also indicated no returns of Sydenham or Pottawatomi river fish closer than 5 km of Telfers Creek. The data suggested that rainbow trout from the southern end of Owen Sound (Sydenham and Pottawatomi rivers) have a high degree of reproductive and perhaps feeding isolation from Telfers Creek, and behavioral imprinting may prevent them spawning in Telfers Creek. Recapture data from tagged rainbow trout of the Nottawasaga River also showed little straying from the stream of initial marking (Berst and Wainio 1967). Dodge (1972) also reported a higher degree of straying among planted rainbow trout. Fifty-one recaptures of the 2500 marked rainbow trout planted in the estuary of the Sydenham River included 43% in the Sydenham River, 39% in adjacent streams less than 1 km from the point of release, and the remainder (18%) 3–73 km from the point of release.

Subsequent recoveries of smolts marked in Black River, tributary to Lake Michigan, demonstrated that at least 84% of the fall spawning run and 66% of the spring spawning run originated in the Black River (Stauffer 1972). These percentages were probably underestimated because of indications that the marks may have caused significant mortality. Returns of jaw-tagged smolts to Black River indicated some straying (Stauffer 1955). Of the 54 fish recovered, 94% returned to Black River and 6% were caught in streams 100–200 km from the Black River. The amount of straying may have been considerably greater than the recovery rate indicated because no effort was expended to recover tags in streams other than Black River. Shetter (1938, 1965) reported on the recoveries of tagged adults in Big Manistee and AuGres rivers, tributaries to Lake Michigan. In these streams most recoveries occurred in the stream of initial marking, although recaptures occurred in other streams during spawning time.

Homing and straying of rainbow trout in two Lake Superior tributaries (Kadunce and Kimball creeks) in Minnesota were observed by Hassinger et al. (1974). Of the 1064 marked smolts, 31 were recovered as adults during a 5-yr period following marking. Twenty-four (77%) returned to the stream of initial marking and seven returned to adjacent streams. Eight tagged adult rainbow trout were recovered in two streams on subsequent spawning runs with six returning to the stream of initial spawning experience.

Winter (1976), who radio-tagged fall-run rainbow trout along Minnesota's north shore of Lake Superior, found that a high percentage (89%) of these fish left the streams during fall–winter and returned to the same rivers the following spring, suggesting they selected a specific stream to spawn. Winter also conducted a displacement experiment with spring-run radio-tagged rainbow trout, releasing 10 in each of two streams (A and B), 10 km apart from the stream of initial capture. No trout returned to the stream where they were tagged, suggesting no 'homing.' In stream 'A,' 90% of the displaced fish ran stream A. In stream 'B,' 30% ran stream B and 70% ran five other streams. He postulated that the lack of homing among the displaced fish may have resulted from (1) stream of initial capture was not the home stream, (2) angler capture prevented return to home stream, (3) favorable stream conditions outweighed imprinting, (4) lack of imprinting, (5) returning adults may have difficulty distinguishing natal stream because of close proximity, and rainbow trout may be imprinted to a region rather than specific stream.

Life Histories

Adults — On the basis of similar sampling periods the 18 study populations were grouped into six time periods: 1928, 1942, 1950–59, 1961–65, 1965–70, and 1970–79. Data from the fall run were combined with those from the run of the following spring.

The age composition of the spawning populations from the study tributaries was fairly uniform irrespective of sampling time, lake, or physical characteristics of the stream (Table 3). The total age of the spawning populations from all tributaries varied from 1 to 8 yr. However, in all tributaries the spawning populations were comprised mainly of 3, 4, or 5-yr-old fish except for those from Black River and McIntyre River where 2- and 6-yr-old fish were more abundant. Fish from the Black River were the youngest (mean age 2.9 yr), mainly 2- and 3-yr-old fish. The oldest fish (5.0 yr) were from the McIntyre River.

Eighteen categories of life history were identified among the spawning populations (Table 3). All of the spawning populations had more than 50% of the population in age categories 2/1, 2/2, and 2/3, except for those from Colpoys and Stokely creeks where the values were 36 and 44%, respectively. In Colpoys Creek, age category 1/3 was more abundant than age categories 2/1, 2/2, or 2/3 and in Stokely Creek, age categories 1/2 and 1/3 were more abundant than age category 2/1. In most tributaries, percentages in age categories other than 2/1, 2/2, and 2/3 were less than 15%.

The duration of stream residence before descent to the lake, among the spawning populations from the study tributaries, ranged from 0 to 4 yr. The percentage of fish in each year of stream residence for the study tributaries was similar. In all tributaries, more than 50% of the population had a 2-yr smolt history, except those from Colpoys Creek where 1-yr-old smolts were more abundant than 2-yr-old migrants. Few tributaries had either 0- or 4-yr smolts. The percentage of spawners with a 3-yr smolt history was generally less than 10% except for Kadunce/Kimball Creeks and Sydenham River where values were 27 and 18%, respectively. Spawners with a 1-yr smolt history were most abundant (46%) from AuGres River (1951, 1955) and Colpoys Creek, and least abundant 0% from Big Creek (Table 3).

Number of males per 100 females, among the spawning populations from all the study tributaries, varied from 24 for the Nottawasaga River to 170 for Telfers Creek and had a median value of 64 (Table 4). Irrespective of sampling date, lake, or physical characteristics of the stream, female dominance was present in most of the study tributaries. The exceptions were in the Pottawatomi River where the sex ratio was approximately 1:1 and in Colpoys Creek, Sydenham River, Telfers Creek, and Black River where the sex ratios favored

TABLE 3. Comparison of the percentages of the spawning populations of the Great Lakes study tributaries according to the different age categories. The mean age for the various spawning populations is also shown.

Date	Tributary	Lake	Age category (Years in stream/years in lake)																	Mean age,[c] yr
			0/3	0/4	1/1	1/2	1/3	1/4	1/5	2/0	2/1	2/2	2/3	2/4	2/5	3/0	3/1	3/2	3/3	3/4	
1928–30	Little Mainstee	Michigan																		3.6
1942	Platte	Michigan			1						37	28	19	12			1	1	1		4.1
1942	AuGres	Huron				2	3				35	36	18	1			3	2			3.8
1951, 1955	AuGres	Huron			15	26	4	1			26	19	7	1				1			3.4
1950–58[a]	Black	Michigan			24	12	1				49	10	2				1	1	1		2.9
1958–59	Silver	Huron			23	2	1	2			21	33	10	2			3	3			3.5
1961–65	Kadunce/Kimball	Superior			2	3	6				8	30	20	3			3	13	12		4.5
1961–65	Nottawasaga	Huron				1				1	27	53	10	1			3	3	1		3.6
1967–70	Batchawana Bay	Superior			10	12	12	3	1		18	17	17	6	1		2	1			3.9
1967–68	Huron	Superior			3	10	6	4			8	24	34	7				2	2		4.3
1969[b]	Platte	Michigan			6	20	16	1			12	30	15								3.5
1968–70	Little Manistee	Michigan			1	3	17	3			3	36	30	7							4.4
1965–70	Telfers (Bothwells)	Huron			10	7	3	1		7	22	22	15	6	2	2	2	1			3.7
1966–70	Pottawatomi	Huron			7	9	5	1			20	27	15	2			5	6	2		3.9
1966–70	Sydenham	Huron			13	10	1			6	30	18	3	1		1	14	3			3.3
1965–70	Nottawasaga	Huron				2	2				11	47	23	5			1	6	2	1	4.3
1965–66	Big Creek	Erie								2	34	27	24	2			2	6	3		3.7
1974–76	McIntyre	Superior					3	5	2		2	21	30	29				2	2	4	5.0
1970–75	Stokely	Superior			3	15	14	7	2		7	20	17	7	1		1	2	2		4.3
1978	Colpoys	Huron	4	1	3	12	21	10			5	13	18	3	2			4	4		4.3
1971–77	Nottawasaga	Huron				1					12	31	33	12	2		1	3	3		4.6
1978–79	Lucknow	Huron			2	7	13	4	2		5	25	26	11	4				1		4.5
1974–79	Ganaraska	Ontario			1	1	4	3	2		9	27	32	14	3		1	1	1		4.5
1970–74	Big Creek	Erie			1	1	2	1			19	32	28	8			2	5	1		4.4
1976–79	Little Manistee	Michigan																			3.9
			$\bar{x}$<1	<1	5	7	6	2	<1	1	18	27	19	6	1	<1	2	3	2	<1	

[a]Sampled in 1950, 1953–54, 1957–58 only.
[b]Fall run only.
[c]Includes fish whose total age was known, but years of stream life or lake life was unknown.

TABLE 4. Comparison of the number of males per 100 females among the spawning populations of the Great Lakes study tributaries, the percentages of the spawning populations according to the number of spawnings and according to the number of years spent in the lake to reach sexual maturity.

				Number of spawnings										
				Maiden	Repeat spawners				Lake years					
Date	Tributary	Lake	M/F×100	1	2	3	4	5	0	1	2	3	4	5
1942	Platte	Michigan	37											
1942	AuGres	Huron	51											
1950–58[a]	Black	Michigan	137											
1958–59	Silver	Huron	83	84	13	3								
1961–65	Kadunce/Kimball	Superior	60											
1961–65	Nottawasaga	Huron	44											
1967–70	Batchawana Bay	Superior	82	67	26	3				17	49	31	3	
1968	Huron	Superior	64											
1967–70	Platte	Michigan	56											
1967–70	Little Manistee	Michigan	78	76	20	4								
1965–70	Telfers (Bothwells)	Huron	170	60	28	9	3		10	52	36	2		
1966–70	Pottawatomi	Huron	96	58	34	7	1		6	59	33	2		
1966–70	Sydenham	Huron	124	82	15	3			14	65	20	1		
1965–70	Nottawasaga	Huron	24											
1965–70	Big Creek	Erie	63											
1974–76	McIntyre	Superior	40											
1978	Colpoys	Huron	120	52	36	10	1	1		21	57	17	5	
1970–77	Nottawasaga	Huron	28											
1978–79	Lucknow	Huron	82	51	36	12	1			15	54	28	2	1
1974–79	Ganaraska	Ontario	67	64	23	12	1			24	47	25	4	
1970–74	Big Creek	Erie	47	39	57	4								
		Median	64											

[a]Sampled in 1950, 1953–54, 1957–58 only.

males.

From all the study tributaries more than 50% of the spawners were maiden fish, except for Big Creek where only 39% of the spawners were maiden trout (Table 4). Among the repeat spawners, the highest percentage were fish from Big Creek where 57% had spawned twice. The Ganaraska and Lucknow rivers had the highest percentage of fish (12%) that spawned three times. In all populations fewer numbers spawned four times and one female in Colpoys Creek spawned five times.

Irrespective of their years of residence in the stream, fish spend 0–5 years in the lake to reach sexual maturity (Table 4). However, most spawners spent 1 or 2 years in the lake to reach sexual maturity. Only a few tributaries had fish that required 4 and 5 years in the lake to reach maturity.

The length measurements of the spawners from the study tributaries are shown for each sex in Table 5 and for each age category in Table 6. For some populations length measurements were fork lengths and for others they were total lengths. It was not possible to convert one measurement to the other because of insufficient data. For each tributary, the average length of female fish was generally greater than that for males (Table 5). For both sexes relatively small fish were from Batchawana Bay, Sydenham River, Nottawasaga River (1961–65, 1966–70), Black River, and Kadunce/Kimball Creek and large fish were from the McIntyre River, Nottawasaga River (1971–78), Pottawatomi River, Colpoys Creek, Lucknow River and Little Manistee River.

As expected, the length of fish from all tributaries increased with age (Table 6). Further, the slower growth rate in the stream environment compared to the more rapid growth in the lake resulted in fish that have spent more than 1 year in the stream being smaller at all subsequent ages. Thus, for each total age the size of fish was inversely related to the duration of stream residence. For example, fish from the Ganaraska River that were 3 yr of age with 1, 2, and 3 years of stream duration had an average fork length of 44, 41, and 26 cm, respectively. A similar age–length relation was observed for all other tributaries (Table 6).

On the basis of both sex and age category relatively small fish were from the Huron River, Black River, Kadunce/Kimball creeks, and Batchawana Bay and large fish were from Little Manistee River and Pottawatomi River. In other tributaries there was no agreement between the large and small fish grouped on the basis of sex and age category. This disparity could be accounted for by difference in sex ratios, size of males and females (female dominance increased the size of fish in the age category), and sample size (fewer fish measurements for age category).

Stream-resident juveniles — Biomass of juvenile rainbow trout from Great Lakes tributaries ranged from about 3 to 114 kg/ha. Lake Superior tributaries ranged from 3 to 114 kg/ha (Shannon 1979; Stauffer 1977). Lake Michigan tributaries ranged from 29 to 77 kg/ha (Taube 1975) and Lake Huron tributaries from 29 to 39 kg/ha (Alexander and MacCrimmon 1974). Despite a considerable range in biomass of juvenile rainbow trout, age-class distributions were quite similar. Lake Superior tributaries were comprised of 75–95% age 0, 6–21% age 1, 1–3% age 2, and 1% age 3 (Shannon 1979; Stauffer 1977). Lake Michigan tributaries contained 68–81% age 0, 18–29% age 1, and 1–3% age 2

TABLE 5. Comparison of the mean fork length (A) or mean total length (B) of male and female rainbow trout spawning populations among the study tributaries.

Date	Tributary	Lake	Male		Female	
			$\bar{x}$	Range	$\bar{x}$	Range
		A. Fork length (cm)				
1961–65	Nottawasaga	Huron	49	(22–74)	54	(32–74)
1967–70	Batchawana Bay	Superior	46		51	
1965–70	Telfers (Bothwells)	Huron	47	(21–77)	55	(20–82)
1966–70	Pottawatomi	Huron	56	(20–76)	60	(25–79)
1966–70	Sydenham	Huron	47	(21–24)	52	(31–77)
1965–70	Nottawasaga	Huron	50	(23–76)	52	(28–79)
1974–76	McIntyre	Superior	51	(37–52)	55	(11–71)
1978	Colpoys	Huron	57	(38–71)	61	(46–74)
1970–78	Nottawasaga	Huron	56	(33–77)	61	(25–82)
1978–79	Lucknow	Huron	60	(25–81)	60	(32–80)
1974–79	Ganaraska	Ontario	47	(20–81)	55	(11–94)
		B. Total length (cm)				
1942	AuGres	Huron	56		57	
1950–58[a]	Black	Michigan	46		52	
1961–65	Kadunce/Kimball	Superior	51	(34–66)	56	(41–68)
1969[b]	Platte	Michigan	56		56	
1967–70	Little Manistee	Michigan	65		68	
1965–70	Big Creek	Erie	54	(20–66)	59	(25–74)
1970–74	Big Creek	Erie	54	(46–66)	59	(41–69)

[a]Sampled in 1950, 1953–54, 1957–58 only.
[b]Fall run only.

(Taube 1975). Lake Huron tributaries were comprised of 84% age 0, 16% age 1, and less than 1% age 2 (Alexander and MacCrimmon 1974).

Differences in growth rate were evident between lake basins. In Lakes Michigan and Huron tributaries, juvenile trout at first and second annulus were 70–100 mm and 160–170 mm, respectively. Lake Superior tributary juvenile trout were 50–60 mm at age 1, 110–140 mm at age 2, 150–171 mm at age 3, and 183–203 mm at age 4. The size differences among Great Lakes tributaries were probably caused by differences in latitude. Within a stream growth rates appeared inversely related to density, at least for Lake Superior tributaries. Young-of-the-year growth was rapid during the first summer, with juveniles in Lake Superior tributaries increasing from 23 to 100 mm in length (Smith 1974). Lake Huron tributary (Telfers Creek) young-of-the-year grew from 30 to 70 mm in a 1-mo period (Dodge 1967).

Downstream migration of juveniles occurred in the spring. This emigration of smolts occurred in the period April–July generally at night, on receding water levels with temperatures of 9–17°C (Stauffer 1972; Alexander and MacCrimmon 1974). Peaks of emigration in Lake Superior tributaries occurred May 29–June 11 (Hassinger et al. 1974), in Lake Michigan tributaries May 21–June 30 (Stauffer 1972), and in Lake Huron tributaries May 15–June 15 (Alexander and MacCrimmon 1974). Early emigration of the older, larger smolts was noted in Lake Michigan and Lake Huron but not in Lake Superior tributaries.

Emigrating smolts varied in length from 64 to 244 mm and in age 1–3 yr. Smolts in Lakes Huron and Michigan tributaries were younger and larger at the same age than those in Lake Superior. Smolts in Lake Superior tributaries were comprised of 88–95% age 1 and 2, with mean lengths of 110–133 mm at age 1, and 138–185 at age 2 (Kwain 1971; Hassinger et al. 1974). Lake Michigan smolts were comprised of 98% age 1 and 2 with mean lengths of 112 mm at age 1 and 180 mm at age 2 (Stauffer 1972). Lake Huron smolts were comprised of 99% age 1 and 2 (Alexander and MacCrimmon 1974). Although large numbers of smolts emigrated at age 1 in Great Lakes tributaries, a review of the stream life age of returning adults indicated that most had spent 2 years of stream life before emigrating. The higher return of age 2 smolts indicated better survival of these smolts during their lake life (Dodge and MacCrimmon 1970; Stauffer 1972; Alexander and MacCrimmon 1974; Hassinger et al. 1974).

Conclusions and Recommendations

This paper has examined rainbow trout populations that enter tributaries to the Great Lakes to determine if this naturalized species, recognized as an admixture of wild and domestic strains of various geographic origins, is comprised of discrete spawning populations or stocks. Our work involved the comparison of timing of spawning and migrations and life history characteristics of rainbow trout populations from widely separated watersheds throughout the Great Lakes. If marked timing of migrations and life history differences were present among the various populations, then it would support the concept that rainbow trout populations in the Great Lakes are comprised of discrete stocks.

Our data revealed some differences in the timing of migration and spawning. In six tributaries to Georgian Bay of Lake Huron (Telfers Creek, Pottawatomi River, Sydenham River, Bighead River, Indian Brook and Beaver River), the timing of migration was autumn, winter, and spring. This was in contrast to all other populations where the timing of migration

TABLE 6. Comparison of the mean fork length (A) or total length (B) of the spawning populations of the Great Lakes study tributaries according to age category.

Date	Tributary	Lake	Age category																				
			0/3	0/4	1/0	1/1	1/2	1/3	1/4	1/5	1/6	2/0	2/1	2/2	2/3	2/4	2/5	2/6	3/0	3/1	3/2	3/3	3/4	4/1	4/2
A. Fork length (cm)																									
1958–59	Silver	Huron				33	45	54	60				38	54	60	65				46	61	66			
1961–65	Nottawasaga	Huron				47	51	63	69			35	47	60	64	68			29	49	62	66			
1967–70	Batchawana Bay	Superior				31	42	53	54	67	75		35	45	51	53	74			36	47		57		
1965–70	Telfers (Bothwells)	Huron	63			35	46	57	59			30	47	57	63	69	72	74	34	57	64	69			
1966–70	Pottawatomi	Huron				35	49	59	61	65	74	33	52	61	67	73	74			57	66	70	74	64	
1966–70	Sydenham	Huron				38	48	59				32	49	59	66		74			52	60	74		59	67
1965–70	Nottawasaga	Huron				33	49	58	67				43	56	64	69	75			43	59	69	69		
1974–76	McIntyre	Superior						53	61	65			38	51	57	66					51	63	69		
1970–75	Stokely	Superior				29	46	53	59	63	68		35	45	51	53	74			36	47		57		
1978	Colpoys	Huron	56	64		46	51	58	66				46	58	66	71	71				58	63			
1970–77	Nottawasaga	Huron					52	56					44	56	65	69	73	75		48	62	66	73		
1978–79	Lucknow	Huron					53	60	63	69			46	56	62	67	71	71			59	65			
1974–79	Ganaraska	Ontario				34	44	54	59	67	70	25	41	48	59	64	69	73	26	47	53	63	65		
B. Total length (cm)																									
1942	AuGres	Huron					54	58					46	58	66	70				59	58				
1951, 1955	AuGres	Huron				39	56	58					46	58	64						61				
1950–58[a]	Black	Michigan				36	50	55	69				42	52	60	64				47					
1961–65	Kadunce/Kimball	Superior	51	56		37	46	56	62				41	53	59	68				43	56	63	66		
1967–68	Huron	Superior				25	48	54	63	66				51	58	64	66			37	58	62	72		
1969[b]	Platte	Michigan				40	58	68					44	59	66										
1968–70	Little Manistee	Michigan				36	59	72	73				46	67	74										
1965–66	Big Creek	Erie											31	47	60	65	69		33	51	62	69	64		
1970–74	Big Creek	Erie					48	59	61				48	58	60	64				47	60	60			

[a]Sampled in 1950, 1953–54, 1957–58 only.
[b]Fall run only.

was autumn and spring. Furthermore, two Georgian Bay tributaries, Telfers Creek and Bighead River, and the tributaries, Normandale Creek (Lake Erie), McKenzie River (Lake Superior), and Platte River (Lake Michigan) had timings of spawning that were different from all other populations. Populations from these tributaries spawned immediately after the autumn run and after the late winter or spring migration. In all other populations there was no autumn spawning, and spawning occurred only after the spring migration. The marked differences in timings of migration and spawning of these populations provide support for the concept that rainbow trout populations in the Great Lakes are developing discrete stocks. Further, Dodge (1972) showed that fish from adjacent streams did not spawn in Telfers Creek. He concluded that a distinct spawning population has been established in this stream. This conclusion was supported by Behnke (1972). It may be that the other populations with autumn spawning or winter migrations are in earlier stages of progression towards the development of discrete stocks, but have yet to be detected.

The interaction of water temperature with stream discharge, both changing with latitude, appeared to influence timing of upstream migrations of rainbow trout especially in the springtime. Fish moved upstream in both spring and fall during conditions of rising water levels, rarely moved at peak freshet, and once again started upstream on decreasing stream discharges (Dodge 1972). Once upstream at suitable spawning facilities, water temperatures controlled spawning activity. Late autumn–early winter spawning occurred in tributaries where fish were offered an acceptable combination of spawning substrate, discharge, and temperature. The combination occurs rarely in Great Lakes tributaries because most fall migrants cannot ascend to "warmer" headwaters because of natural and artificial barriers. It is unlikely that physiological readiness accounts for the lack of autumn spawning as most males and at least some females observed in autumn runs are near or at spawning maturity. Consequently, most rainbow trout populations with autumn runs spawn in springtime only, in water conditions influenced by warming air temperatures and less by groundwater discharge (Dodge 1972).

The timing that we observed for rainbow trout runs into tributaries to the Great Lakes was similar to that of the west coast of North America reported by Ricker (1972). In the west coast, steelhead runs are usually protracted, particularly into large rivers. A winter run (December–March) occurs frequently, and is most important in shorter coastal streams. These fish spawn from late winter into early spring. A spring run occurs in some rivers between March and May, fish spawning as soon as they reach suitable habitat. In some coastal streams and in several large rivers a summer rush of fish appears. Commonly large animals, these fish winter-over and spawn in the following spring. If one allows for minor differences in seasons between the West Coast and Great Lakes regions, then the winter and spring runs in both areas are probably the same phenomenon. As well, the spring runs spawn at similar times in both regions, and, in at least two Georgian Bay streams, trout from winter runs spawn at the same time as they would on the West Coast. With some further imagination, it is possible to relate the West Coast summer runs with Great Lakes fall runs, accepting some differences in discharge patterns and stream temperatures. Furthermore, fall-run Great Lakes fish usually overwinter to spawn in the following spring as do their West Coast cousins.

Ricker (1972) suggested that both seasons of return and spawning are controlled genetically. Accepting this hypothesis, it is likely that the great variance in seasons of migrations and spawning of rainbow trout in the Great Lakes is a manifestation of the influence of a variety of environmental factors affecting many types, races, stocks, etc., of rainbow trout (*Salmo gairdneri*) from the West Coast. It might be, too, that the occurrence of some of the autumn–winter populations can be explained by the geneology of the fish planted in the areas of the Great Lakes where these anomalies were observed.

Homing in rainbow trout populations of the Great Lakes appears to be as highly developed as that described for steelhead on the West Coast (Shapovalov and Taft 1954; Ricker 1972, among others). In the Great Lakes rainbow trout appear to return to either a specific stream (presumably natal), or to a local geographical area. Homing to geographical areas rather than specific streams may occur where streams are close and physical and chemical conditions of the streams are similar. This return to localized areas could result in searching patterns, with environmental conditions of the individual streams determining the final selection of a spawning stream. Imprinting to a region could account for the widespread establishment of a rainbow trout throughout in the Great Lakes. Consequently, homing in the Great Lakes could produce locally discrete spawning stocks of rainbow trout in single streams such as Telfers Creek (Dodge 1972) or to local geographical areas such as Minnesota's North Shore (Winter 1976).

Rainbow trout populations in all five Great Lakes exhibited great variability in life histories. However, this variability among rainbow trout in the Great Lakes was very similar to that for steelhead trout populations on the west coast of North America (Maher and Larkin 1955; Withler 1966; Narver 1969) and for those in the Finger Lakes Region, New York (Hartman 1959). It appears that rainbow trout in the Great Lakes have retained the major characteristics of their life history from their native range.

This review has pointed out the great variability among populations of rainbow trout in the Great Lakes, and the innate ability of these populations to respond to a wide range in environmental factors (Allendorf and Utter 1979). These characteristics, together with this species' ability to 'home,' provide rainbow trout populations in the Great Lakes with the potential to evolve, over time, discrete stocks adapted to similar yet discrete and specific habitat.

The available evidence indicates that full use of complex river systems by salmonids, giving maximum production of young fish from the system and maximum returns to it, is achieved only when a complex of stocks is present (Larkin 1972). If this is the case, then the management of rainbow trout in the Great Lakes should foster the emergence of discrete stocks. Consequently, the management of rainbow trout in the Great Lakes should be based on individual characteristics of each population and environmental characteristics of its natal stream. For example, angling seasons and harvests should be managed according to known migration and spawning times of the various populations. Also, tributary streams supporting rainbow trout populations should be protected to maintain the essential spawning and rearing habitat for the

various populations.

To date, the success of rainbow trout in the Great Lakes has been more "good luck" than "good management." Firstly, a diverse gene pool was used for the original introductions (MacCrimmon and Gots 1972); every recognizable rainbow trout "type" from northern California to central British Columbia was transferred to hatcheries and natural waters in the Great Lakes Basin. Secondly, after initial introductions, the species was left alone to adapt to its new environment. The apparent lack of success of the early introduction to the Great Lakes of rainbow trout convinced fish managers that plantings had failed. Subsequently, because of this perception and other domestic fish problems, agencies significantly reduced or curtailed the culture of rainbow trout within the Basin. Thirdly, through the Great Lakes Fishery Commission, Canada and the United States undertook sea lamprey control. Dodge (1967) and Berst and Wainio (1967) showed a direct relationship between the increasing success of rainbow trout in certain Georgian Bay streams and the onset of sea lamprey control.

However, there are some fisheries management techniques that might offset the adaptive success of this species in the Great Lakes. Firstly, some managers continue to introduce frequently large numbers of rainbow trout of indeterminate geneology into areas with self-sustaining populations that require only slightly different management than they now receive to achieve naturally a level of harvest that these managers perceive only as possible from hatchery plants. Secondly, the potential use of populations well-adapted to a wide range of environmental factors has to be ignored by fish culturists because disease prevention in hatcheries appears to be more important than stock selection for rehabilitation. Thirdly, the public and administrators have the mistaken belief that fish passes around obstructions in spawning streams are adequate substitutes for no barriers at all. Fish passes in the Great Lakes likely select against the passage of large repeat spawning females, which by their loss of streamlining, cannot negotiate the structure. We have observed that the largest females in the spring creel are caught below fishways. One author (Dodge) caught larger females in trap nets below the fishway than in a fishway on the Sydenham River. Lastly, certain angling seasons in some Great Lakes jurisdictions may be selecting more autumn-run than spring-run adult trout. Before this process continues much further, managers must contrive means of ensuring that those behavioral characteristics (autumn-runs and winter-spawning) are maintained within gene pools. Several late spring seasons that allow extra heavy harvests of spring-run fish may cause such severe depressions in these populations that without a protected fall-run, these local populations may collapse.

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Lake Whitefish (*Coregonus clupeaformis*) Stocks of the Ontario Waters of Lake Huron[1,2,3,4]

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Historical and contemporary data on lake whitefish (*Coregonus clupeaformis*) from the Ontario waters of Lake Huron were examined for evidence of stocks with the objective of defining population boundaries. We delineated the spatial distribution of five stocks from tag–recapture data and the general location of six additional stocks on the basis of population parameters such as growth rate, age structure, and abundance trends.

Samples of fish collected (summer and fall) from 5 of the 11 potential stocks were evaluated on the basis of 11 morphometric and 7 meristic characters. We also examined osseometric features such as shape of scales and otoliths, and electrophoretic characteristics at 32 loci associated with 12 enzyme systems.

The summer and fall samples for each group were generally not significantly different. For the phenotypes examined electrophoretically, each stock was in Hardy–Weinberg equilibrium; 12 of the 32 loci considered were polymorphic and 4 of the 10 possible genetic distances differed significantly from zero.

The Inner Basin stock was distinctly different from all other stocks. The Blind River stock was also found to be different by osseometrics, but not by morphometrics or electrophoresis. Osseometrics separated the stocks by basin of origin. Two stocks, Outer Basin and Burnt Island, appeared to be the most similar and could be separated from each other only on the basis of growth rate and tagging data. These two stocks are adjacent to each other in the main basin of Lake Huron, along the south shore of Manitoulin Island.

Whitefish stocks of Lake Huron represent groups of fish that differ phenotypically and genotypically in varying degrees, are spatially separated, and behave as cohesive units. We conclude that they should be regarded as functional units for management purposes.

Key words: lake whitefish, *Coregonus clupeaformis*, Lake Huron, stocks, tag–recapture data, population structure, morphometrics, meristics, osseometrics, scale and otolith shape, starch gel electrophoresis, biochemical genetic variation

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CASSELMAN, J. M., J. J. COLLINS, E. J. CROSSMAN, P. E. IHSSEN, AND G. R. SPANGLER. 1981. Lake whitefish (*Coregonus clupeaformis*) stocks of the Ontario waters of Lake Huron. Can. J. Fish. Aquat. Sci. 38: 1772–1789.

Les auteurs ont examiné les données historiques et contemporaines sur le grand corégone (*Coregonus clupeaformis*) des eaux ontariennes du lac Huron afin d'y découvrir des signes de l'existence de stocks et de définir les limites des populations. Il leur a été possible de cerner la distribution spatiale de cinq stocks à partir des données de marquages–recaptures et l'aire générale de six autres stocks d'après des paramètres de population tels que taux de croissance, structure par âge et tendances d'abondance.

Onze caractères morphométriques et 7 méristiques ont été utilisés pour évaluer des échantillons de poissons prélevés (été et automne) parmi 5 des 11 stocks potentiels. Des caractéristiques ostéométriques, telles que la forme des écailles et des otolithes ont été examinées, ainsi que les caractéristiques électrophorétiques à 32 loci associées à 12 systèmes enzymatiques.

D'une manière générale, les échantillons d'été et d'automne de chaque groupe ne sont pas significativement différents. Chaque stock est en équilibre de Hardy–Weinberg quant aux phénotypes examinés électrophorétiquement; 12 des 32 loci étudiés sont polymorphes et 4 des 10 distances génétiques possibles diffèrent de façon significative de zéro.

Le stock du bassin Intérieur est nettement différent de tous les autres stocks. On a constaté que le stock de la rivière Blind différait également par ses caractères ostéométriques, mais non morphométriques ou électrophorétiques. L'ostéométrie permet de séparer les stocks selon leur bassin d'origine. Deux stocks, celui du bassin Extérieur et de l'île Burnt, semblent se ressembler le plus et ne peuvent être séparés l'un de l'autre que par le taux de croissance et les données du marquage. Ces deux stocks sont voisins l'un de l'autre dans le bassin principal du lac Huron, le long de la côte sud de l'île Manitoulin.

Les stocks de grands corégones du lac Huron représentent des groupes qui diffèrent à divers degrés phénotypiquement et génotypiquement, sont séparés dans l'espace et se comportent comme unités cohésives. En conclusion, ces stocks devraient être considérés comme unités fonctionnelles aux fins de gestion.

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HISTORICALLY, fishermen have recognized color variants among lake whitefish (*Coregonus clupeaformis*) in their catches from the Ontario waters of Lake Huron. It is important to fisheries management to understand the significance and distribution of these morphs and to know whether they are genetically fixed, or more labile phenotypic expressions of different environmental conditions. Even if these phenotypic differences reflect spatial separation and only partial reproductive isolation among genetically similar stocks, they can provide valuable diagnostic characteristics.

Our purpose was to improve our understanding of the seasonal geographic distribution of Lake Huron whitefish, as indicated by polygenic and single locus (biochemical) characters. We examined tag returns and population dynamics data and studied samples of fish from several locations to characterize morphometric and meristic, osseometric, and electrophoretic variation among these groups of whitefish.

The most direct information describing the spatial distribution and interaction of stocks comes from recapture data from tagged fish released at various locations. The degree of synchrony of population statistics such as growth rate, age composition, and trends in catch statistics also provides useful information on the association of adjacent groups of fish.

Our analysis includes only whitefish of a size vulnerable to commercial fishing gear. We examined fish from areas of the lake where contemporary and traditional fisheries enabled us to collect nearly synchronous samples from comparable gear. There was sufficient evidence from historical observations that whitefish from these areas could at least tentatively be classified as stocks.

We regard a "stock" as a population of fish that behaves as a cohesive unit whose members exhibit common responses to environmental conditions within its geographic boundaries. This includes, but is not restricted to, population units that are reproductively isolated. The opportunity to detect and document differences is confounded by the relatively high degree of phenotypic plasticity of coregonines. Stock discreteness may also be obscured by spatial overlap during various seasons of the year.

Morphometric and meristic data on individuals were examined for evidence of stock discreteness. Although these characters are influenced by environmental differences, they can be as valuable in indicating stock discreteness as other, more genetically related, features.

Calcified structures have been used to identify and discriminate among stocks of fish (e.g. Anas and Murai 1969). An osseometric study (the measurement of calcified structures) that used both scales and otoliths was conducted to determine whether the shapes of these structures might be used to discriminate among groups of whitefish from Lake Huron. Scales were studied, because Jarvis et al. (1978) found that scale shape quantification could be used to differentiate between two stocks of yellow walleye (*Stizostedion vitreum vitreum*) from Lake Erie. Otoliths were also used in the shape

analysis, because their structure is less variable and their growth is less extreme than that of scales and is less influenced by environmental conditions (Casselman 1978).

Biochemical variation, as measured by electrophoresis, is largely uninfluenced by short-term environmental conditions, hence reflects genetic, rather than environmental variation (Allendorf and Utter 1979). Electrophoresis has been used extensively to study intraspecific genetic variation of whitefish (Clayton and Franzin 1970; Clayton et al. 1973; Franzin and Clayton 1977; Imhof et al. 1980). In some studies, the life history and morphological variation has been compared to the genetic variation determined by electrophoresis (Lindsey et al. 1970; Kristofferson 1978; Kirkpatrick and Selander 1979). One of the major objectives of our study was to relate the genetic variability, as measured by biochemical variation, to the osseometric and morphometric variations and compare these results with those obtained from the population studies of spatial distribution and population dynamics.

Materials and Methods

Spatial Distribution and Population Dynamics Studies

Population dynamics data were available on whitefish from 11 locations in the Ontario waters of Lake Huron (Table 1). Tag–recapture data were also available for five of these stocks: Inner Basin (*A*), Outer Basin (*B*), Burnt Island (*C*), Blind River (*D*), and Southern Georgian Bay (*I*), providing the most direct information on the spatial distribution. Tagged whitefish were released by the Ontario Ministry of Natural Resources at various locations and recovered by commercial and experimental fisheries. Sources of information for various parts of the lake include: J. C. Budd, J. B. Smith, and F. E. J. Fry (1963, unpublished report); Budd (1957); Spangler (1974); and Cucin and Regier (1966). We analyzed the distribution of all recaptured fish (taken primarily by commercial fishermen) that had been at liberty 1 mo or longer after tagging from the following areas:

Tagging area	Tagging period	No. tagged	No. of recaptures
Southern Georgian Bay	1956–64	3389	1215
North Channel	1960–66	804	165
Burnt Island area	1964–68	5000+	2038
South Bay (Outer Basin)	1970–79	7155	3090

The distribution of recaptured fish is limited to areas where commercial fisheries were active. Minimum procedures for sampling commercial whitefish catches consisted of: removal of scales for age determinations, fork length measurements of individual fish, a record of total weight of catch, date, and gear employed (gill net or impounding nets).

We have also used population dynamics variables, paired with respect to time of sampling, that reflect the influence of fisheries upon various stocks. Thus, a comparison of growth rates or age and size distributions represents the cumulative effect of natural and fishing mortalities and growth conditions experienced by the respective stocks over the several years prior to the sampling date (Roelofs 1958; Mraz 1964; Collins 1979; Spangler and Collins 1980). These variables should culminate in asynchrony in production trends for areas of the lake containing different stocks.

TABLE 1. Tentative stocks of whitefish of the Ontario waters of Lake Huron. Samples collected in 1979 and 1980 from stocks *A*, *B*, *C*, and *D* to study meristics and morphometrics and from these as well as stock *J* to study osseometrics and electrophoresis.

Stock	Stock code letter	O.M.N.R. statistical district	Lat.	Long.
Inner Basin (South Bay)	*A*		45°37′N	81°54′W
Outer Basin (South Bay and Lake Huron)	*B*	OH-1	45°34′N	82°00′W
Burnt Island (Lake Huron)	*C*	OH-1	45°49′N	82°57′W
Blind River (North Channel)	*D*	NC-1	46°06′N	83°09′W
Clapperton Island (North Channel)	*E*	NC-2	46°00′N	82°12′W
Fraser–Manitowaning Bays	*F*	NC-3	45°55′N	81°42′W
Eastern Manitoulin Island (East Coast)	*G*	GB-1	45°50′N	81°35′W
Off Parry Sound (Georgian Bay)	*H*	GB-3	45°15′N	80°17′W
Southern Georgian Bay	*I*	GB-4	44°44′N	80°40′W
Off Southampton (Mid-Lake Huron)	*J*	OH-3	44°35′N	81°20′W
Off Goderich (Southern Lake Huron)	*K*	OH-4	43°50′N	81°36′W

Length-at-age comparisons were usually based on fish captured in commercial pound nets or gill nets early in the season before growth began. Averages were computed for the largest comparable age-class for each paired sample and were tested by Student's *t*-test. Age compositions of the stocks were compared by applying the Kolmogorov–Smirnov two-sample test to cumulative age distributions converted to percentages. The minimum sample size used in any paired comparison in the population dynamics study was 98, and the maximum was 1639 fish.

Trends in relative abundance of whitefish, for Ontario Ministry of Natural Resources Statistical Districts in which the tentative stocks reside, were inferred from annual whitefish landings for the period 1961–75 (Anon. 1972a, b; Ridgley 1976). Correlation analyses were conducted on catch data from districts containing paired stocks. The absence of a significant correlation ($P > 0.05$) was accepted as an indication of differences between districts and the stocks they contain.

To summarize the evidence for stock differences, a numeric weight was arbitrarily assigned, ranking the parameters in accordance with their importance as follows: tag data 4, mean length-at-age 3, age composition 2, and trends in catch statistics 1.

To examine stock discreteness by morphometric and meristic, osseometric, and electrophoretic techniques, two samples of fish (50 summer and 50 fall) were collected during 1979 from four of the stocks (*A*–*D*) for which tag–recapture data were available. These specimens were used in the morphometric and meristic study. As paired seasonal samples were not available from the fifth tagged stock, Southern Geor-

TABLE 2. List of morphometric and meristic characters and acronyms used in the analyses. Morphometrics were calculated as a percentage of fork length.

Morphometrics	Acronym	Meristics	Acronym
Head length	NHL	Total gill rakers	TGR
Head depth	NHD	Pored lateral line scales	LLP
Interorbital width	NIW	Pelvic rays (principal)	PLRA
Snout length	NSNL	Pectoral rays (principal)	PERA
Maxillary length	NMXL	Anal rays (principal)	ARA
Maxillary width	NMXW	Total branchiostegals, left	LTB
Orbital diameter	NOD	Total branchiostegals, right	RTB
Pectoral fin length	NPCL		
Pelvic fin length	NPVL		
Caudal peduncle depth	NCPD		
Gill-raker length	NGRL		

gian Bay (*I*), samples were obtained in the fall of 1979 and the summer of 1980 from an alternative stock, Southampton (*J*). Specimens from all five stocks (*A*–*D*, *J*) were used in the osseometric and electrophoretic studies.

Samples were collected from fish in their summer habitat, and from fall spawning populations, to measure variability within and among stocks and seasons and to permit comparisons among techniques. Specimens were obtained from commercial nets of various mesh sizes: gill nets (114–127 mm, stretched measure), pound nets (76 mm, crib mesh), and a trap net with 51 mm, crib mesh. Average fork lengths (cm) and scale ages (yr) with ranges (in parentheses) for the 500 samples were as follows:

Stock	Length	Age
A	41.9 (36–49)	9.4 (4–16)
B	49.2 (38–63)	5.3 (4–11)
C	43.6 (26–63)	3.9 (2–11)
D	50.7 (38–61)	5.0 (3–10)
J	45.3 (36–59)	3.6 (2–8)

MORPHOMETRICS AND MERISTICS

A random sample of 30 of the 50 individuals collected at each of four sites (*A*–*D*) was used in this analysis. The original suite of external features consisted of 13 morphometric and 21 meristic characters that have been used in published studies of whitefishes. To meet the requirements of multivariate analysis, the original set was reduced to 11 morphometrics and 7 meristics (listed in Table 2) for final analyses.

Morphometric measurements followed those of Lindsey (1962) with the following exceptions: NHL (Hubbs and Lagler 1958), to the bony margin of the opercle; NDH, distance from the top of head to bottom of jaw vertically through the centre of the eye; NOD, distance from the anterior to the posterior orbital bony margin, horizontally through the center of the eye; NGRL, measured on the raker in the angle of the first left arch. Meristic counts followed those of Hubbs and Lagler (1958) with the following exceptions: LLP, according to Lindsey (1962); PLRA, excluding the first one or two rudimentary rays; and PERA, excluding the first rudimentary ray.

Preliminary analyses revealed that meristic variables contributed minimally to a solution. Therefore, interpretations were based primarily on morphometrics.

Body measurements were expressed as ratios of fork length to remove variations of fish size within each sample. This adjustment for size variation was successful for most samples; only 33% (29 of 88 possibles) showed relationships significantly different from zero. The regression equation accounted for a very small percentage of total variation (r^2 typically less than 0.30); and the slopes of the lines were usually similarly signed. Thus, it was concluded that size variation within sample, when adjusted by fork length, had minimal effect on succeeding analyses. These ratios were used as variables in subsequent analyses.

Analysis of variance was used to compare the variation among samples for individual characters. Direct discriminant function analysis (Klecka 1975), using all characters simultaneously, was used to compare the samples. The sample means, in discriminant space (centroids), were compared for significant differences. The discriminant function was used to classify individual fish into groups. Canonical discriminant functions were used to produce scatterplots to visualize relationships among the individuals of the groups.

From the coordinates of the group centroids in discriminant space, Euclidean distances were calculated for all pairs of groups. These distances were used in an unweighted pair-group arithmetic average (UPGMA) cluster analysis (Sneath and Sokal 1973) to produce dendrograms illustrating the relationships among the groups.

OSSEOMETRICS

Scales and otoliths that were collected from the same fish were used in the study of osseometrics. Scales were removed from a key area on the left side of the body from the row directly above the lateral line, starting directly below the anterior insertion of the dorsal fin and extending for 10 scales towards the posterior. When the scales on the left side were missing or were abnormal, regenerated, or damaged, scales were taken from the corresponding area on the right side of the body (3.0% of the samples), and their images were reversed. Cleaned, air-dried scales (four to six) that were macroscopically symmetrical about the anterior–posterior axis were imprinted on cellulose acetate. The image that was microscopically most symmetrical was photographed at 19× magnification.

TABLE 3. Tissues, enzyme, and buffer systems used in the electrophoretic analyses.

Enzyme system	Acronym	Tissue and buffer system[a]			
		Eye	Heart	Liver	Muscle
Alcohol dehydrogenase	ADH			B or D	
Creatine kinase	CK	A			A
Glucose phosphate isomerase	GPI				A
Glycerol-3-phosphate dehydrogenase	G3P				D
Isocitrate dehydrogenase	IDH			C or D	C or D
Lactate dehydrogenase	LDH	A	A	A	A
Malate dehydrogenase	MDH			B	B
Malic enzyme	ME			B	B
Phosphoglucomutase	PGM				A
Sorbitol dehydrogenase	SDH			A	
Superoxide dismutase	SOD			A	A
Xanthine dehydrogenase	XDH			E	

[a]Buffer system: A, discontinuous Tris-citric acid (gel pH 8.5) lithium hydroxide–boric acid (tray pH 8.1) Ridgway et al. (1970) as modified by Allendorf et al. (1977). B, citric acid-*N*-(3-aminopropyl)-morpholine (pH 6.1) Clayton and Tretiak (1972). C, Ayala et al. (1973) as modified to pH 6.1 with Tris-HCl by May et al. (1979). D, Tris-citric acid (pH 8.0) Clayton and Gee (1969). E, Tris-boric acid-EDTA (pH 8.7) Markert and Faulhaber (1965).

Scale age of all samples was assessed independently by two interpreters; agreement was 98%.

The otoliths were removed from the cranium, and the right one was placed in a solution of 65% glycerol and 0.5% thymol. The lateral side of this otolith was subsequently photographed at 38× magnification. If the right otolith could not be located, or was damaged or abnormal (e.g. crystalline), the left one was used (2.5% of the samples) and the image was reversed. This photographic image transformed the lateral view of the otolith into a planar image.

All scale and otolith data were extracted from these photographic images and were collected directly by use of a digitizer integrated with a PDP-11 minicomputer.

Several reference features were established on the scale and otolith images. The scale focus was used, because on whitefish scales it can be located easily and precisely. The anterior scale radius (ASR) was drawn from the focus to a point on the anterior edge at the midpoint of the anterior lobe. The posterior scale radius (PSR) was obtained by extending this line from the focus to the posterior edge. Since the nucleus in the intact otolith was often difficult to see and could not be precisely located, an artificial focus was located on the otolith image. The focus was located at the midpoint of a line joining the extreme anterior tip with the extreme posterior tip. The anterior otolith radius (AOR) was a line joining the anterior tip and the focus.

The shape analysis used involves a procedure of planar shape quantification that is essentially the same as that used by Jarvis et al. (1978), with some minor modifications. The perimeter was unrolled about the focus, rather than the centroid, in a counterclockwise direction from an axis of rotation (zero — azimuth), starting from the posterior radius of the scale (PSR), and from the anterior radius of the otolith (AOR). In these analyses, from 1 to 20 harmonics (k) were used. Each harmonic is described by two shape component variables: amplitude (A_k) and phase angle (ϕ_k). The harmonic amplitude was divided by the mean radial length to adjust for size; hence, each shape was corrected to a circle of unit radius. The variance (C_k) for each harmonic was also calculated, and indicates the percentage contribution of the kth harmonic. The variance provides a measure of the goodness-of-fit between the observed shape and the model shape constructed by the kth harmonic.

Multiple discriminant function analysis (Klecka 1975) was used to assess the degree of difference among the samples by using these vector variables for the scale and otolith shapes.

Scale shape among young, middle-aged, and old fish was significantly different (J. M. Casselman unpublished data). To eliminate any bias, only scales and otoliths from fish of 4 or 5 yr of age were used. Too few samples of fish of these ages were available from the Inner Basin sample, so some 6-yr-old fish from that stock were included. Sample sizes were too small to conduct direct comparisons of summer and fall samples by these analytical techniques.

ELECTROPHORESIS

Tissue samples were taken from the fish used for the morphometric and osseometric studies. The techniques of Tsuyuki et al. (1966) and May et al. (1979) were used to perform horizontal starch gel electrophoresis on fresh or frozen samples. Protein variation for 32 loci belonging to 12 enzyme systems was assayed. The tissues, and enzyme and buffer systems used are described in Table 3. The specific protein staining techniques followed those of Allendorf et al. (1977) with the addition of 0.2% brilliant blue R as a general protein stain for CK. For the microtechnique staining for MDH, the diethanolamine stain buffer of Clayton et al. (1971) was used.

Twelve of the 32 loci examined were found to be polymorphic. Of these polymorphic loci, five (G3P-1; LDH-3 or 4; CK-1; PGM-2; SOD) had rare alleles (frequencies ≤ 0.01). These alleles were not used in the subsequent analyses. For the liver IDH-3,4 polymorphism, a genetic model suggested by J. W. Clayton (Department of Fisheries and Oceans, Freshwater Institute, Winnipeg, Man., personal communication) fitted phenotypic frequencies obtained for fresh livers from parents and their progeny. However, zymograms

obtained from frozen, stored livers did not give consistent results, because of changes in the activity of the isozymes associated with IDH-3. For most of the samples used in this study, it was necessary to freeze the livers prior to the electrophoretic analysis, hence, the liver IDH-3 polymorphism had to be excluded from the analysis. Further, no satisfactory genetic model to fit parent and offspring data has been found for the ME-2 polymorphism. This locus was also omitted, leaving a total of 30 loci for subsequent analyses.

For the remaining six polymorphic loci (G3P-1; IDH-4; LDH-2; LDH-4; MDH-3,4), parent and offspring data fitted genetic models that have already been described (G3P-1 corresponds to G-3-PDH B locus, Clayton et al. 1973; MDH-3,4 to Franzin and Clayton 1977; LDH-1,2 to Imhof et al. 1980; LDH-3,4 to Clayton and Franzin 1970; IDH-3,4 to J. W. Clayton personal communication; P. E. Ihssen unpublished data).

Summer and fall samples of 50 fish from each of the five stocks ($A-D$, J) were assayed. For IDH-4, the livers for all the summer 1979 samples (except Inner Basin) and the fall 1979 samples for Southampton gave very low activity because of improper frozen storage, and could not be used in the analysis.

The phenotypic proportions of the samples were tested for Hardy–Weinberg equilibrium by using a maximum likelihood ratio test (Sokal and Rohlf 1969). For MDH-3,4, for which the isozymes of the two loci cannot be differentiated, expected phenotypic proportions were calculated using a maximum likelihood method outlined by Imhof et al. (1980). Expected phenotypic proportions for MDH-3,4 were also calculated assuming equal allelic frequencies for each locus. Assuming this, it is not necessary to be able to differentiate allelic products from the two loci, and allelic frequencies can be obtained directly from the phenotypic proportions.

Allelic and phenotypic proportions for each enzyme system were compared between seasons and among stocks by using homogeneity χ^2 tests based on maximum likelihood ratios (Sokal and Rohlf 1969). Simultaneous χ^2 tests were performed using a method outlined by Cooper (1968).

Genetic distances and average heterozygosities, based on 30 loci, were calculated using a method outlined by Nei (1978). The relationships among the stocks were illustrated by using UPGMA cluster analysis on the genetic distances (Sneath and Sokal 1973).

Results and Discussion

Spatial Distribution and Population Dynamics Studies

The distribution of tag recaptures for five stocks: Inner Basin (A), Outer Basin (B), Burnt Island (C), Blind River (D), and Southern Georgian Bay (I) (Fig. 1), indicate that most whitefish do not migrate great distances. This observation is consistent with the findings for Lake Michigan (Smith and Van Oosten 1939; Roelofs 1958; Imhof et al. 1980), Lake Superior (Dryer 1964) and southern Georgian Bay (Cucin and Regier 1966). Ninety-five percent of the recaptures were taken within relatively confined areas, described by the vertical bars illustrated in Fig. 1. The most interesting result is that closely adjacent stocks, such as Inner Basin (A) and Outer Basin (B) South Bay stocks, which are separated by less than 2 km, are different stocks. This confirms the contention of J. C. Budd, J. B. Smith, and F. E. J. Fry (1963, unpublished report) that the Inner Basin stock (A) and Outer Basin stock (B) are discrete, even though no physical barrier exists between the basins except for a possible thermal barrier during late summer (McCombie 1967). Budd (1957) reported that whitefish from the Outer Basin South Bay stock (B) moved along the east coast of Manitoulin Island in Georgian Bay (District GB-1) and southward along the west shore of the Saugeen Peninsula (OH-2). The return from this area of fewer than 1% of the Outer Basin tagged fish suggests that, although fisheries were relatively inactive there during our study, only a very small proportion of this stock leaves the vicinity of South Bay. We cannot determine, at this time, the magnitude of the northward migration (dashed line, Fig. 1); however, the paucity of South Bay tag returns from an intensive fishery along the south shore of Manitoulin Island (OH-1) clearly showed that there was no significant westward movement of whitefish from South Bay. Similarly, of the other stocks, only a few tagged individuals strayed beyond the boundaries depicted in Fig. 1, indicating that there was a low level of mixing between adjacent stocks.

Comparisons between sample areas of mean length at age, age composition, and catch statistics show some differences between the 11 stocks (Table 4). Stock indices for individual pairs varied with time in response to changes in population characteristics, but this approach is useful for identifying stocks in the absence of tagging data. While a high stock index creates confidence that the stocks differ, a low stock index value does not necessarily mean that stocks being compared are the same. The lowest index value of 1 pertains to the comparison between Blind River stock (D) and the Goderich stock (K) which are separated by several hundred kilometers and are clearly spatially separate stocks.

Morphometrics

Analysis of summer samples from four stocks ($A-D$) showed significant differences among stock centroids (Wilk's $\lambda = 0.124$, $\chi^2 = 232.5$, df $= 33$, and $P < 0.001$). Two functions were significant and accounted for 97.3% of total variance. Function 1 (Fig. 2(i)), accounted for 77.8% of the variance, and separated the Inner Basin stock (A) from the remainder on the basis of contrasts between NIW, NOD, NMXW, NPCL, and NCPD. That is, Inner Basin fish (A) have larger head and pectoral fin dimensions, but smaller caudal peduncle depths. Function 2 (19.5%) partially separated the Burnt Island stock (C) from the remaining three groups on the basis of a contrast between NIW, NMXL, NPCL, and NSNL, NMXW, NPVL. That is, Burnt Island fish (C) tend to have narrower interorbital widths; shorter maxillaries, and pectoral fins; and longer snouts, maxillaries, and pelvic fins. The Inner Basin stock (A) was very different from the Outer Basin (B), Blind River (D), and Burnt Island (C) stocks, which were similar, with the latter somewhat different from the other two (Fig. 2(i)).

A measure of the discriminating power and classification accuracy of these functions may be gathered from an a posteriori classification of individual specimens using the derived discriminant functions. Two functions correctly assigned 75% of the individuals to their proper stocks.

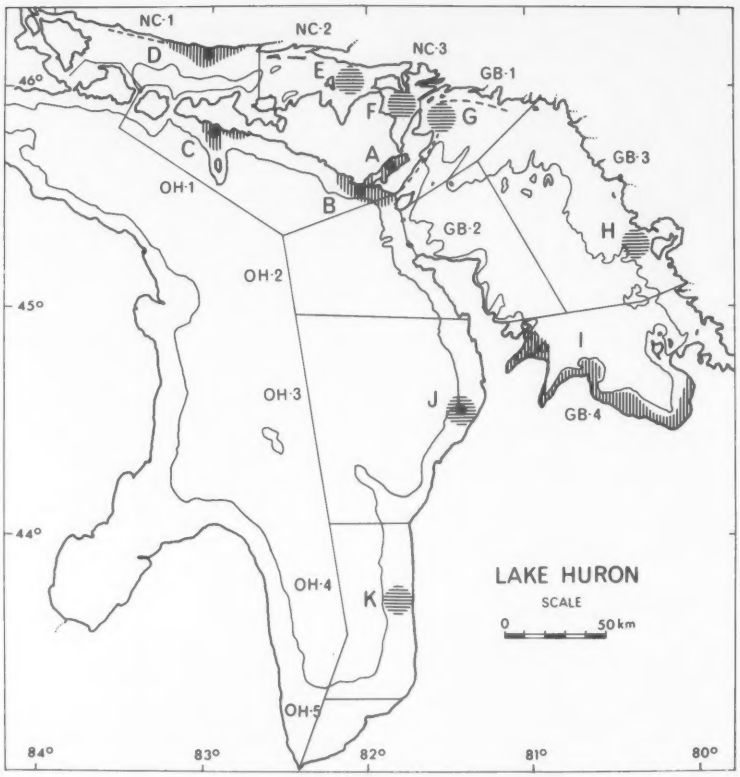


FIG. 1. Lake Huron with Ontario Ministry of Natural Resources Statistical District OH-1-5, North Channel NC-1-3, and Georgian Bay GB-1-4. Whitefish stocks are indicated by code letters $A-K$ and are described in Table 1. Vertical bars represent stock boundaries defined by tag recaptures, and horizontal bars show stocks with undefined boundaries. Black dots describe areas sampled for morphometric and meristic, osseometric, and electrophoretic characteristics. The contour line is the 40 m isobath.

The dendrogram (Fig. 2(i)) indicated that the fish from the Inner Basin stock (*A*) were distinctly different from the cluster containing the Outer Basin (*B*), Burnt Island (*C*), and Blind River (*D*) stocks. Also, samples from Outer Basin (*B*) and Blind River (*D*) clustered closer to one another than either did to Burnt Island (*C*).

Analysis of fall samples from four stocks ($A-D$) showed significant differences among centroids (Wilk's $\lambda = 0.121$, $\chi^2 = 235.3$, df = 33, and $P < 0.001$). Two functions were significant and accounted for 97.7% of total variance. Function 1 accounted for 92.4% of the variance, and separated Inner Basin (*A*) fish from all others on the basis of contrasts between NHL, NOD, NMXW, and NCPD (Fig. 2(ii)). Function 2 (5.2%) showed no clear trends.

Centroid position in discriminant space and the high degree of overlap indicated that the Blind River (*D*), Outer Basin (*B*), and Burnt Island (*C*) stocks were similar, and Inner Basin (*A*) was quite different. A posteriori classification correctly assigned 70.8% of the individuals.

The dendrogram also indicated that Inner Basin stock (*A*) was distinctly different from the cluster containing the other three stocks ($B-D$) (Fig. 2(ii)), and the Blind River stock (*D*) was somewhat different.

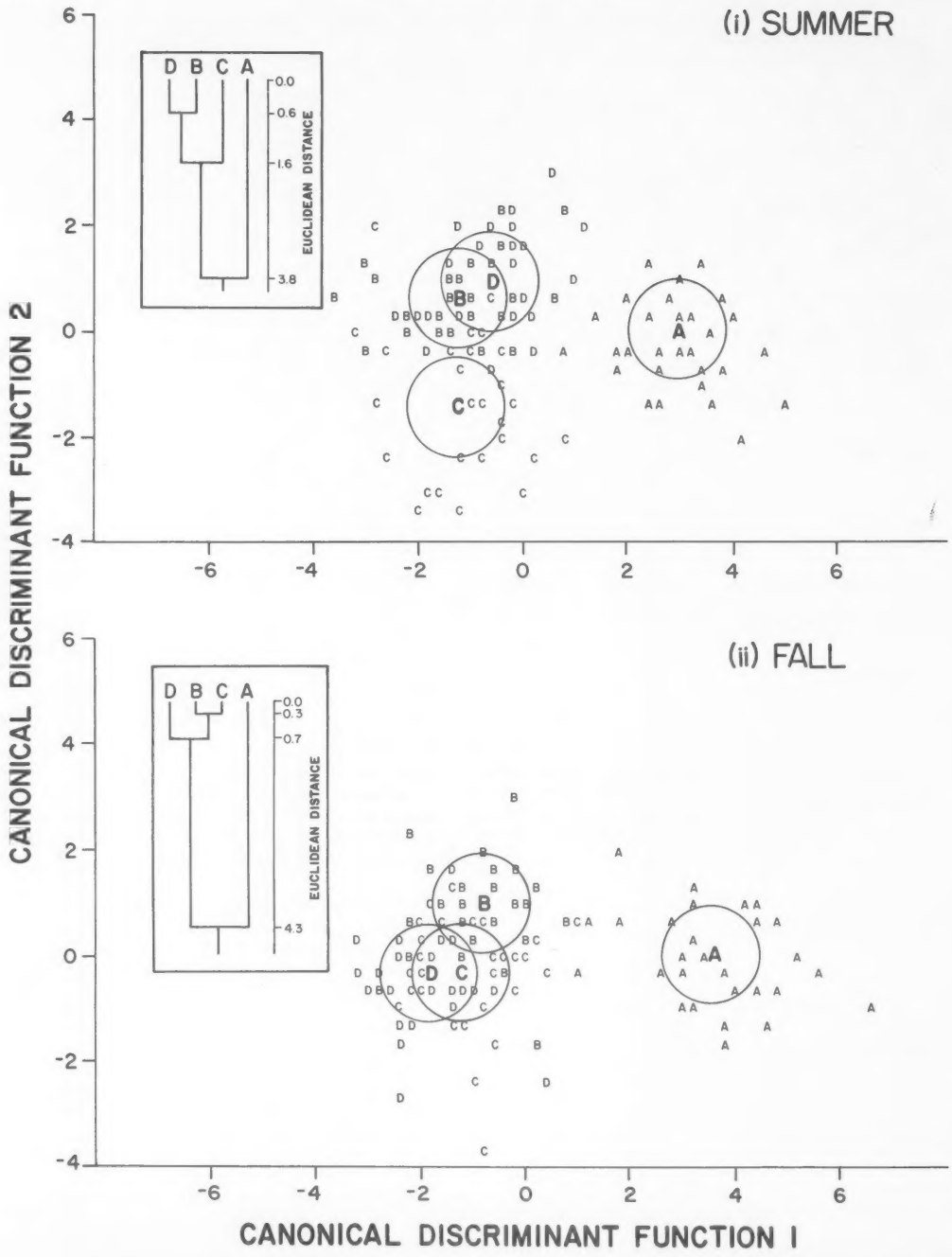
Direct comparison of the analyses for summer and fall samples (Fig. 2(i) and 2(ii)) is impossible, since the functions generated are not equivalent. However, overall variation and variation within the stocks ($A-D$), as evidenced by positioning on the standardized discriminant axes, was greater in the fall samples. Also, the actual overlap of results from Inner Basin (*A*), with those of Outer Basin (*B*), Burnt Island (*C*), and Blind River (*D*) stocks was less in the fall sample. The Euclidean distance at which Outer Basin (*B*), Burnt Island (*C*), and Blind River (*D*) stocks were clustered was less in the fall (0.7) than in the summer (1.6). The distance at which the Inner Basin stock (*A*) was joined to the other stocks was similar in the two seasons (summer 3.8, fall 4.3).

Discriminant function analysis that combined both seasons and samples from each of the four stocks preserved the dis-

TABLE 4. Comparison of whitefish from Lake Huron based on samples paired with respect to time and capture gear. Plus indicates a significant difference between stocks and minus no difference. Blank indicates no data.

Stock comparisons	Code letter		Parameter value 4 Tag data	3 Mean length at age[a] ($P<0.05$)	2 Age comp. ($P<0.05$)	1 Catch[b] corr. coeff. ($P<0.05$)	Stock index	Sample[c] period
Inner Basin	*A*							
Outer Basin		× *B*	+	+(7)	−		7	June 1950
		B	+	+(6)	+		9	May 1973
Burnt Island		*C*	+	+(6)	+		9	May 1973
Blind River		*D*	+	+(6)	+		9	May 1973
Southern Georgian Bay		*I*	+	+(6)	+		9	May 1973
Outer Basin	*B*							
		× *C*	+	+	−		7	May 1973
		D	+	+	−	+	8	May 1973
		I	+	+	−	+	8	May 1973
Burnt Island	*C*							
		× *D*	+	−	−	+	5	May 1973
		I	+	+	−	+	8	May 1973
Blind River	*D*							
Clapperton Island		× *E*	+	+(3)	−	−	7	Sep. 1966
		E	+	+(3)	−	−	7	July 1968
Fraser−Manitowaning bays		*F*		+	+	+	6	May 1959
		F		−(5)	+	+	3	May 1960
Eastern Manitoulin Island		*G*		+	−	+	4	May 1959
		G		+	+	+	6	May 1960
		G		−	+	+	3	May 1961
Parry Sound		*H*		+	−	+	4	May 1960
		H		+	−	+	4	May 1961
		I	+	+	+	+	10	May 1960
		I	+	−	+	+	7	May 1961
		I	+	+	−	+	8	May 1973
Goderich		*K*		−	−	+	1	May 1960
Fraser−Manitowaning bays	*F*							
		× *G*		−	+	+	3	May 1959
		G		−	+	+	3	May 1960
		H		+	+	+	6	May 1960
		I	+	−	+	+	10	May 1960
		K		+	+	+	6	May 1960
Eastern Manitoulin Island	*G*							
		× *H*		+	−	−	3	May 1960
		H		+	+	−	5	May 1961
		I	+	+	+	+	10	May 1960
		I	+	+	−	+	8	May 1961
		K		+	+	+	6	May 1960
Parry Sound	*H*							
		× *I*	+	+	+	−	9	May 1960
		I	+	+	+	−	9	May 1961
		K		+	−	+	4	May 1960
Southern Georgian Bay	*I*							
		× *K*	+	+	+	+	10	May 1960
Southampton	*J*							
Goderich		× *K*		+	−	+	4	May 1979

[a]All comparisons were made between fish of age 4 unless otherwise indicated by age in parentheses.
[b]Correlation coefficients based on annual catch data from statistical districts which stocks inhabited for period 1961−75.
[c]Samples are from commercial gill nets with the exception of 1950 pound net sample.


(i) SUMMER
D B C A
0.0
0.6
1.6
3.8
EUCLIDEAN DISTANCE
(ii) FALL
D B C A
0.0
0.3
0.7
4.3
EUCLIDEAN DISTANCE
CANONICAL DISCRIMINANT FUNCTION 2
CANONICAL DISCRIMINANT FUNCTION 1

tinctness of the Inner Basin (*A*) samples and indicated considerable overlap of the other samples. Results of ANOVA analyses for each character confirmed the results obtained by discriminant function and phenetic analyses.

At different times of the year, there are quantifiable morphometric differences between these four whitefish stocks. Fish taken in summer differ in morphometric but not meristic characters from those taken in fall.

The degree of separation between the four stocks (*A*–*D*) was not as high as expected. This was true even in fall when it was hypothesized there should be the greatest uniformity within the stocks and the greatest separation between stocks. Four possibilities exist: (1) variation is not genotypic; (2) the fall sample did not contain spawning groups; (3) spawning groups contain individuals with different genotypes; and (4) the samples were not truly representative of the stocks.

Although statistically significant differences among whitefish from the four locations were found, the results of this morphological examination do not provide convincing evidence for biologically significant differences among these stocks. This discrepancy between the statistical and the biological interpretations is probably the result of experimental design, especially sample size. Variation in size distribution of individuals between samples required correction (morphometric character/fork length). The adequacy of this correction for discriminant function analysis is questionable. Any variation in size remaining after this correction could provide another source of discrepancy between the statistical and biological interpretations.

Several populations of whitefish in North America (Lindsey et al. 1970; Bodaly 1979) and Scandinavia (Svärdson 1979) are distinguishable by bimodal counts of gill rakers. There are parapatric "dwarf" and "normal" forms of this species for which there have been different decisions regarding degree of relationship (Lindsey 1963; Fenderson 1964; Kirkpatrick and Selander 1979). Even at the species level it is considered by some to be a single variable form, and by others to be part of a species complex. Thus, by the nature of the species, stock discrimination is difficult.

Gill rakers are the morphological character most frequently used for distinguishing or separating whitefishes, and modal numbers can be used to separate populations in the same lake that have achieved a certain level of genetic distinction (Lindsey 1963). In the present study of morphological characters, there were no significant differences between seasons for any area. There was a slight significant difference between areas for fall samples only. The total spread of gill-raker numbers encountered was eight (24–32) and there was no significant difference in modal values. Hence, gill rakers alone will not distinguish among individuals of these stocks.

Considering all the parts of the morphological examination, the only consistent conclusion is that the whitefish can be divided into two groups — one group that includes only those from the Inner Basin (*A*) of South Bay, and one group that includes whitefish from the Outer Basin (*B*) of South Bay, Burnt Island (*C*), and Blind River (*D*).

Osseometrics

Multiple discriminant function analyses of the shape vector variables for both scales and otoliths revealed differences among the stocks. In all four scale and otolith discriminant analyses, the first two discriminant functions were highly significant, and for the two structures accounted for a similar percentage of the total variance: scales 86.7%; otoliths 86.8%.

The broadest comparison, which combined males and females collected in summer and fall, used shapes of structures from 239 whitefish (Fig. 3(i)). Using the *F* statistic, all scale shape comparisons between stocks were significantly different ($P < 0.05$) except for that between Burnt Island (*C*) and Southampton (*J*) ($P > 0.05$). Otolith shapes gave similar results; however, otoliths from both the Inner Basin (*A*) and Blind River (*D*) fish were distinctly different ($P < 0.01$). In these comparisons, shape of the Outer Basin (*B*) otoliths was not significantly different from those of either the Burnt Island (*C*) or Southampton (*J*) stocks.

In these analyses, 58.6% of the scale shapes and 54.9% of the otolith shapes were correctly assigned to their appropriate stock. Of the remainder, 44% of the scale shapes and 56% of the otolith shapes were correctly assigned to their appropriate stock as a second choice. The Inner Basin stock (*A*) was most successfully classified: scales 72.7%; otoliths 73.3%.

To eliminate variability between the sexes and seasons, more specific comparisons were conducted. The differences among stocks for scales and otoliths from male whitefish were highly significant ($P < 0.01$) (Fig. 3(ii)). However, scale and otolith shapes of the Outer Basin (*B*) and Burnt Island (*C*) stocks and scale shapes of the Burnt Island (*C*) and Blind River (*D*) stocks were significantly different, but at a lower probability level ($P < 0.05$). This comparison among males resulted in a more successful classification of "grouped" shapes for scales (68.3%), and particularly for otoliths (78.0%). The Inner Basin stock (*A*) was the most successfully classified by both scales (76.9%) and otoliths (89.3%).

Shape analysis of structures from female fish substantiated that the Blind River stock (*D*) was significantly different from three of the other stocks (Fig. 3(iii)). The Southampton stock (*J*) was different from the Outer Basin (*B*) and Burnt Island (*C*) stocks. Stocks were equally well classified by scales (68.0%) and otoliths (70.6%). The Blind River stock (*D*) was most successfully classified: scales 76.9%; otoliths 80.8%.

Analyses of fall samples indicated that the Outer Basin (*B*) and Burnt Island (*C*) stocks were similar, and the Blind River stock (*D*) was different (Fig. 3(iv)). This was more apparent for otoliths than for scale shapes. As with the other more specific comparisons, more of the grouped shapes were classified correctly: scales 74.5%; otoliths 76.5%. Some fall sam-

FIG. 2. Discriminant function scatterplots and phenograms based on morphometrics of whitefish from Lake Huron. Phenograms based on UPGMA clustering of Euclidean distances and for both data sets the cophenetic correlation coefficient = 0.99. Some points represent multiple plots. (i) Summer, data from 120 fish from four stocks (*A*–*D*). (ii) Fall, data from 120 fish from four stocks (*A*–*D*). *A*, Inner Basin; *B*, Outer Basin; *C*, Burnt Island; *D*, Blind River. Ⓐ, Centroids with 1 SD.

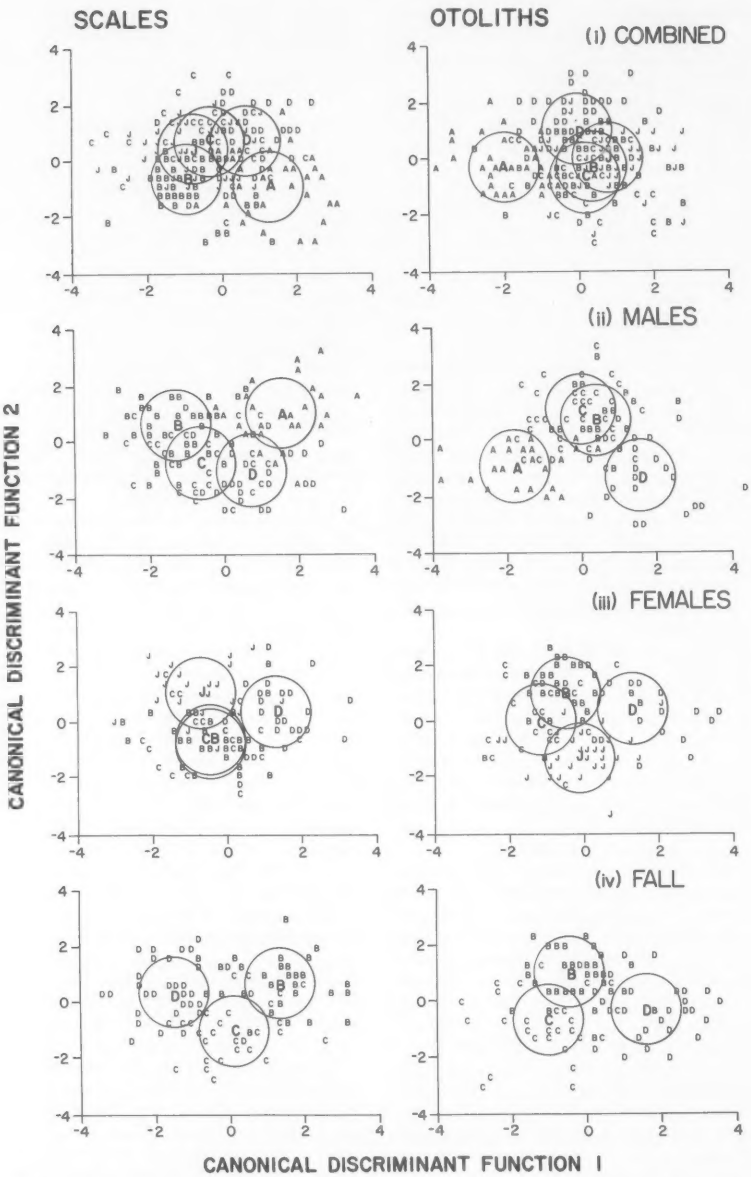


FIG. 3. Discriminant function scatterplots using the shape vector variables for 20 harmonics for scales and otoliths of whitefish from Lake Huron. Some points represent multiple plots. (i) Combined, data from 239 fish, both sexes and seasons, from five stocks ($A-D$, J): scales, $n = 239$; otoliths, $n = 233$. (ii) Males, data from 120 fish from four stocks ($A-D$): scales, $n = 120$; otoliths $n = 118$. (iii) Females, data from 103 fish from four stocks ($B-D$, J): scales, $n = 103$; otoliths, $n = 102$. (iv) Fall, data from 104 fish from three stocks ($B-D$): scales, $n = 104$; otoliths, $n = 102$. *A*, Inner Basin; *B*, Outer Basin; *C*, Burnt Island; *D*, Blind River; *J*, Southampton. Ⓐ, Centroids with 1 SD.

TABLE 5. Percent frequency of occurrence of the probability levels of the F statistic for comparisons between stocks using shape vector variables for scales and otoliths.

Probability level	Stock				
	Inner Basin *A*	Outer Basin *B*	Burnt Island *C*	Blind River *D*	Southampton *J*
<0.001	92.9	41.7	37.5	62.5	35.7
0.01–0.001	7.1	20.8	20.8	25.0	21.4
0.05–0.01		20.8	20.8	12.5	21.4
>0.05 (NS)		16.7	20.8		21.4
<0.01	100.0	62.5	58.3	87.5	57.1
Number of comparisons	14	24	24	24	14

ples of these stocks could be identified by the shapes of their calcified structures from 80 to 85% of the time (scales 85.3% (*D*); otoliths 79.4% (*B*)). Jarvis et al. (1978) obtained a similar level of classification (80%) for walleye scales when they compared two samples of 5-yr-old male fish taken during the same spawning period.

Otolith shape is slightly better than scale shape for discriminating among these stocks of whitefish. However, scale and otolith results were similar, and were combined to examine the overall differences using the probability level resulting from comparisons between stocks (Table 5). Shape vectors for the structures were significantly different for all comparisons involving both Inner Basin (*A*) ($P < 0.01$) and Blind River (*D*) ($P < 0.05$) stocks. The other three stocks were less distinct ($P < 0.05$, Outer Basin (*B*), 83.3%; Burnt Island (*C*), 79.2%; Southampton (*J*), 78.6%).

Statistically typical structures for each stock were selected from the two most extensive discriminant analyses. These structures were the best examples of each stock, because they had the highest probability of stock membership (closest to the centroid). The probability of membership was higher for the otoliths ($\bar{x} = 0.895$, range 0.753 (*B*) – 0.994 (*A*)), than for the scales ($\bar{x} = 0.802$, range 0.606 (*J*) – 0.992 (*A*)).

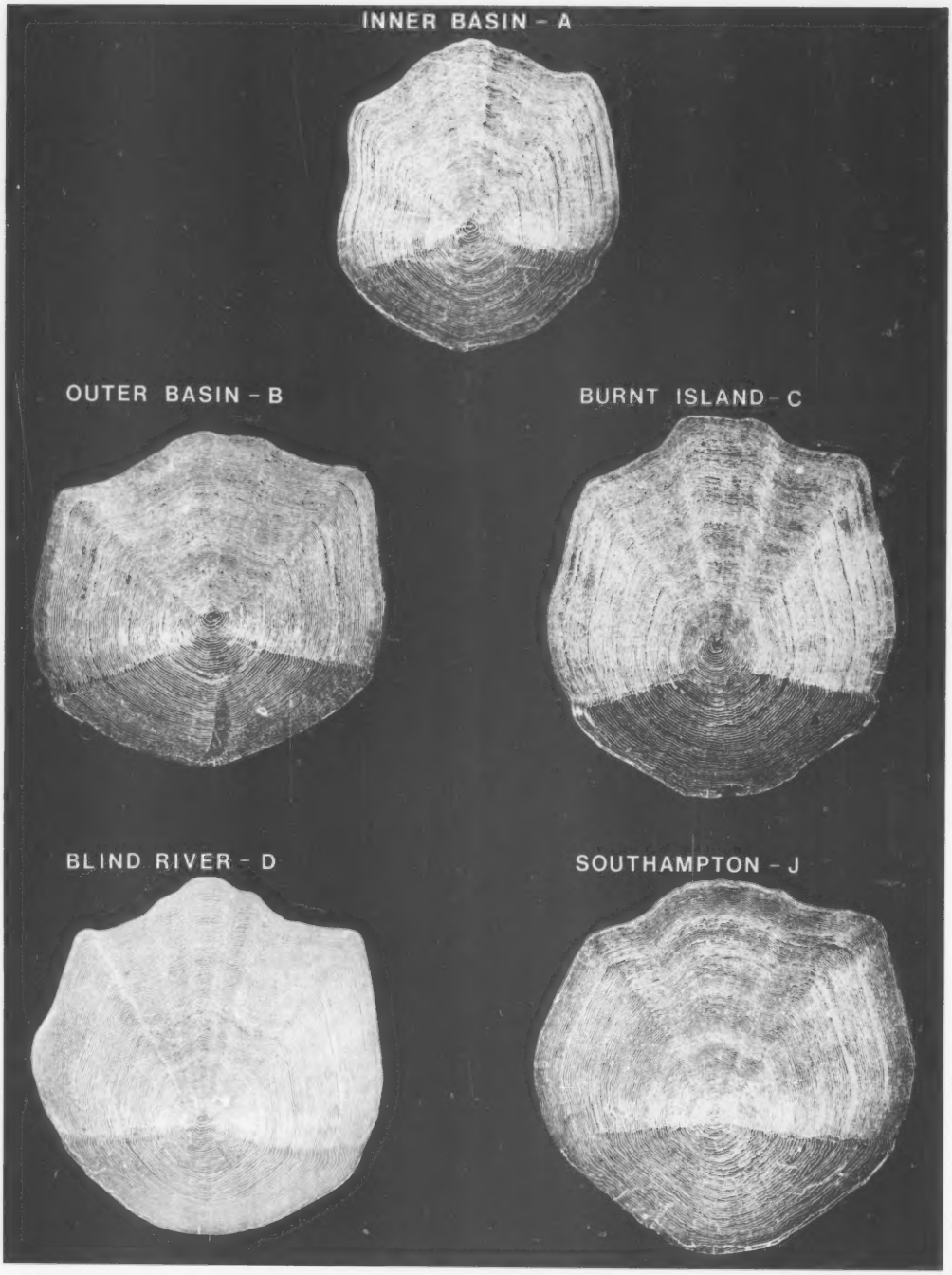
Typical scales for each of the five stocks are illustrated in Fig. 4. Whitefish scales are basically round ($\bar{C}_1 = 89.5\%$, range 71.3% (*B*) – 97.7 (*D*)), but are also slightly oval ($\bar{C}_2 = 5.9\%$, range 0.42% (*D*) – 17.8% (*B*)). In whitefish scales, the explained variance of the first two harmonics was ~ 95% and of the first 10 harmonics 99%. Jarvis et al. (1978) found that in walleye scales, 30.8 and 40.9% of the variance was explained by the second and third harmonics, respectively. The amplitude of the second harmonic and the phase angle of the third harmonic were the scale vector components with the highest discriminating powers. Considering the 10 most powerful discriminating variables, amplitude and phase angle were selected in approximately equal numbers. The lower-order harmonics had higher discriminating powers in scale shape, since ~ 85% of the 10 best shape discriminators were represented by fewer than 10 harmonics.

Typical otoliths for each stock are illustrated in Fig. 5. Whitefish otoliths are basically oval ($\bar{C}_2 = 66.1\%$, range 61.7% (*D*) – 73.4% (*A*)), but are also quite round ($\bar{C}_1 = 15.8\%$, range 10.3% (*A*) – 20.1% (*J*)), and somewhat quadrangular in shape ($\bar{C}_4 = 9.6\%$, range 8.9% (*J*) – 10.5% (*C*)). The first, second, and fourth harmonics combined explained ~ 90% of the variance. As in scales, 10 harmonics explained ~ 99% of the variance. The amplitude of the fifth harmonic and the phase angle of the sixth harmonic were the two otolith shape vector components with the highest discriminating powers. Of the first 10 variables with the highest discriminating powers, 65% were phase angles. The lower- and higher-order harmonics were equally important discriminators of otolith shape.

The osseometric phase of the study grouped the five tentative stocks into three groups. The Inner Basin stock (*A*) was distinctly different, the Blind River stock (*D*) was moderately different, and the remaining three stocks, Burnt Island (*C*), Southampton (*J*), and Outer Basin (*B*) were similar and least distinct. In this third grouping, the Outer Basin stock (*B*) appeared to be slightly different from the other two. This grouping separated these five stocks according to the basin of origin — South Bay, North Channel, and main basin of Lake Huron.

ELECTROPHORESIS

In the electrophoretic studies, no evidence was found for deviation from Hardy–Weinberg equilibrium for any of the five tentative stocks or any seasonal sample of these stocks. Out of 46 samples assayed, three (Blind River, fall; MDH-3,4, $\chi^2_2 = 9.14$: Burnt Island, summer; MDH-3,4, $\chi^2_2 = 9.02$: Inner Basin, fall; G3P-1, $\chi^2_2 = 8.18$) had phenotypic proportions differing significantly from Hardy–Weinberg equilibrium at the 5% level. To test whether these three significant deviations are expected at the 5% level, a simultaneous χ^2 test as outlined by Cooper (1968) was applied to the data. If one considers the different enzyme systems and the samples for each season to provide independent tests of deviation from Hardy–Weinberg equilibrium for each population separately, then there are 9 tests for each stock (10 for Inner Basin). The modified significance level was $\alpha_{0.05} = 0.05/9 = 0.006$ (Inner Basin; $\alpha_{0.05} = 0.05/10 = 0.005$). Since the three samples that were found to differ significantly from Hardy–Weinberg equilibrium individually have $P > 0.01$, clearly they cannot be regarded as significant for 9 (or 10) simultaneous tests. For MDH-3,4, either gametic frequencies or allelic frequencies (assuming equal frequencies at each locus) gave similar significance levels in the above analysis. Hence, subsequently MDH-3,4 was treated as two loci with equal allelic frequencies at each locus.


INNER BASIN – A
OUTER BASIN – B
BURNT ISLAND – C
BLIND RIVER – D
SOUTHAMPTON – J

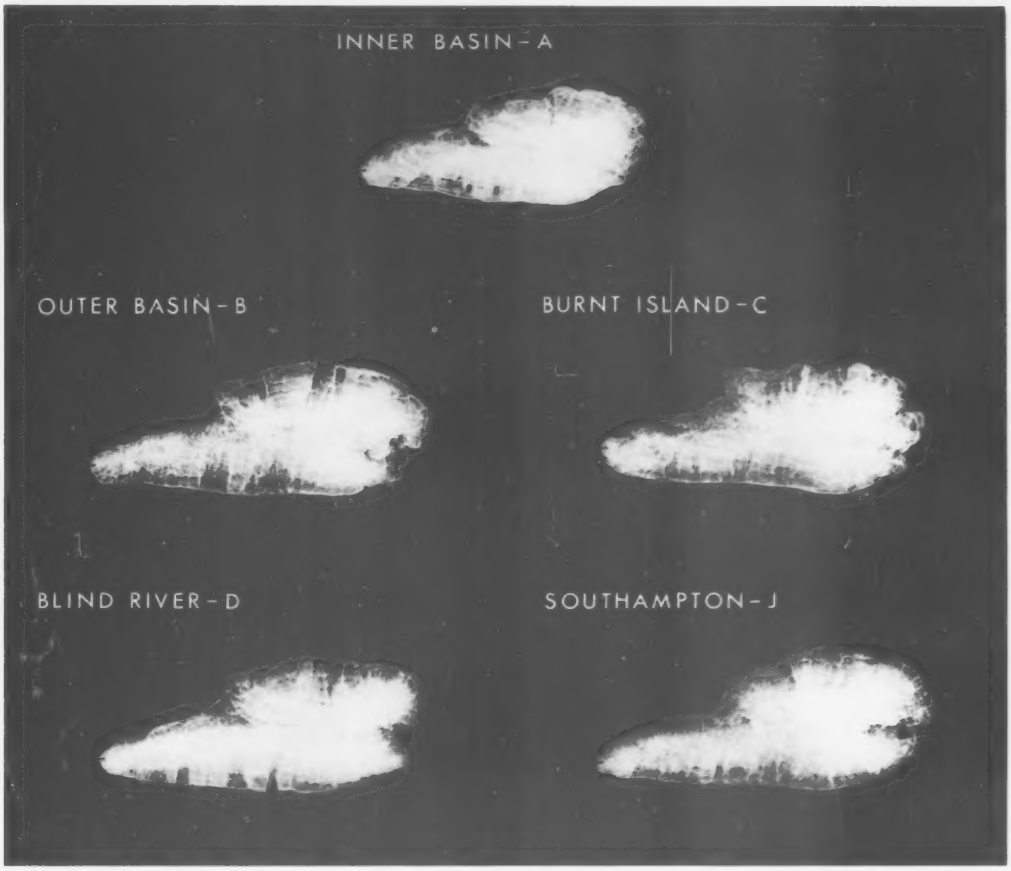


FIG. 5. Typical otoliths from each of the five stocks of whitefish. The probabilities of membership are Inner Basin (*A*), 0.994; Outer Basin (*B*), 0.753; Burnt Island (*C*), 0.935; Blind River (*D*), 0.952; and Southampton (*J*), 0.839. Dark line on the left edge marks the anterior of the otolith and the point about which the otolith shape was unrolled in a counterclockwise rotation (zero — azimuth). (×6).

The fall and summer samples for each stock and each enzyme system had nonsignificantly different phenotypic and allelic frequencies. Out of 21 seasonal comparisons, only one (Burnt Island, LDH-2) was significant at the 5% level (Table 6). In a simultaneous χ^2 test, the significance level of this one sample in 21 was found to be nonsignificant. Hence, the seasonal samples represented the same, or very similar, genetic stock with respect to these enzyme systems. This analysis does not rule out the possibility that significant differences would have been detected if larger sample sizes of both individuals and loci (particularly loci, see Nei 1978) had been assayed.

The summer and fall samples were combined for each of the five stocks and their phenotypic and allelic frequencies compared for individual loci or duplicate pair in the case of MDH-3,4. The phenotypic and allelic comparisons gave similar significance levels. For MDH-3,4, LDH-2, and LDH-4, the stocks had highly significantly different frequencies ($P < 0.005$) and for G3P-1 and IDH-4, the stocks were not significantly different at the 5% level (G3P-1, $0.10 < P < 0.25$; IDH-4, $0.50 < P < 0.75$). The overall χ^2 values for allelic and phenotypic frequencies were $\chi^2_{24} = 66.5$, $P < 0.001$ and $\chi^2_{25} = 103.1$, $P < 0.001$, respectively. The results for MDH, LDH, and G3P are similar to those of Imhof et al. (1980) for

FIG. 4. Typical scales from each of the five stocks of whitefish. The probabilities of membership are Inner Basin (*A*), 0.992; Outer Basin (*B*), 0.934; Burnt Island (*C*), 0.706; Blind River (*D*), 0.771; and Southampton (*J*), 0.606. White line on the ventral edge marks the posterior of the scale and the point about which the scale shape was unrolled in a counterclockwise rotation (zero — azimuth). (×6).

TABLE 6. Allelic frequencies for protein variants of five stocks of whitefish from Lake Huron.

Stock	Sampling date	MDH-3,4[a]			G3P-1			IDH-4			LDH-2			LDH-4		
		82[b]	100	n[c]	82	100	143	100	119	n	97	100	n	100	130	n
Inner Basin A	Fall 1979	0.365	0.635	50	0.306	0.469	0.224	0.776	0.224	49	0.080	0.920	50	0.890	0.110	50
	Summer 1979	0.335	0.665	50	0.320	0.480	0.200	0.814	0.186	43	0.060	0.940	50	0.920	0.080	50
Outer Basin B	Fall 1979	0.220	0.780	50	0.330	0.470	0.200	0.775	0.225	40	0.040	0.960	50	0.920	0.080	50
	Summer 1979	0.255	0.745	50	0.340	0.460	0.200				0.030	0.970	50	0.830	0.170	50
Burnt Island C	Fall 1979	0.260	0.740	49	0.250	0.580	0.170	0.745	0.255	47	0.030	0.970	50	0.950	0.050	50
	Summer 1979	0.315	0.685	50	0.224	0.541	0.235				0.100	0.900	50	0.920	0.080	50
Blind River D	Fall 1979	0.250	0.750	50	0.340	0.530	0.130	0.756	0.244	41	0.080	0.920	50	0.930	0.070	50
	Summer 1979	0.232	0.768	50	0.390	0.450	0.160				0.100	0.900	50	0.970	0.030	50
Southampton J	Fall 1979	0.310	0.690	50	0.350	0.490	0.160				0.020	0.980	50	0.980	0.020	50
	Summer 1980	0.335	0.665	50	0.320	0.480	0.200	0.750	0.250	48	0.021	0.979	47	0.980	0.020	50

[a]Enzymatic nomenclature is according to Allendorf and Utter (1979).
[b]Allelic products designated by their mobilities relative to the bands reflecting the common allele designated as 100.
[c]Number of fish in the sample.

"sympatric" stocks of lake whitefish in Lake Michigan. They also found the largest frequency differences among their stocks for MDH and LDH, and no significant differences for G3P.

The allelic frequencies for each locus (Table 6), including monomorphic loci, were used to calculate Nei's standard genetic distances between each stock pair and the average level of heterozygosity for each stock (Table 7). Since only 6 out of 30 loci were polymorphic (8 out of 32 if ME-2 and IDH-3 are included) and the differences in allelic frequencies were small (Table 6), the genetic distances were small (Table 7). Only 4 out of 10 distances calculated are significantly different from zero. These distances are similar to those found for sympatric whitefish stocks by Kristofferson (1978) and Imhof et al. (1980), but much smaller than those observed for allopatric stocks of whitefish (Kristofferson 1978; Ihssen et al. 1981) or stocks of other teleosts (e.g. Allendorf 1975; McGlade and MacCrimmon 1979; Grant and Utter 1980; Grant et al. 1980).

The average heterozygosity per locus varied from 0.065 to 0.073 among these five stocks (Table 7). Kirkpatrick and Selander (1979) reported a value of 0.077 for whitefish from the Allegash Basin. These values are within the range usually observed for vertebrates (0.05–0.10, Nei 1975) or teleosts (e.g. *Astyanax* 0.11, Avise and Selander 1972; *Salmo gairdneri* 0.06, Allendorf 1975; *Oncorhynchus nerka* 0.05, Grant et al. 1980).

In the dendrogram (Fig. 6), at the highest branching point Inner Basin (*A*) and Southampton (*J*) stocks are on a separate branch from the other three stocks. None of the three genetic distances among the stocks — Outer Basin (*B*), Burnt Island (*C*), and Blind River (*D*) — are significantly different from zero (Table 7), hence, the other branching points in the dendrogram are not significant. Three out of the four significant genetic distances involve the Inner Basin stock (*A*). The dendrogram obscures the fact that the genetic distances between the Southampton stock (*J*) and the Burnt Island (*C*), Blind River (*D*) stocks are not significantly different from zero.

General Discussion

Analysis of tagging data gave evidence that 5 of 11 groups of whitefish that had been tentatively identified as stocks were behaving as cohesive units and should be regarded as stocks. Population parameters indicated that the other six groups were relatively discrete and probably are stocks.

Other techniques used to examine summer and fall samples differentiated five of these stocks in varying degrees. Seasonal differences were not significant, therefore, the summer and fall samples appeared to represent the same stock. The Inner Basin stock (*A*) of South Bay was distinctly different from all other stocks (Fig. 7). The only exception was the Southampton stock (*J*) which was found to be similar electrophoretically. The Blind River stock (*D*) of the North Channel was osseometrically different from all other stocks. Two stocks (Outer Basin (*B*) and Burnt Island (*C*)) appeared to be most similar and could be separated only on the basis of growth rate and tagging data (Fig. 7). These two stocks are adjacent in the main basin of Lake Huron along the south

TABLE 7. Standard genetic distances and average heterozygosity per locus (Nei 1978) for five stocks of whitefish from Lake Huron. Genetic distances below diagonal and average heterozygosity on the diagonal.

Stock	Inner Basin *A*	Outer Basin *B*	Burnt Island *C*	Blind River *D*	Southampton *J*
Inner Basin *A*	0.0727±0.0307				
Outer Basin *B*	0.00057±0.00053	0.0668±0.0286			
Burnt Island *C*	0.00021±0.00015	0.00026±0.00029[a]	0.0681±0.0289		
Blind River *D*	0.00076±0.00056	0.00000±0.00026[a]	0.00021±0.00037[a]	0.0656±0.0280	
Southampton *J*	0.00002±0.00027[a]	0.00051±0.00047	0.00008±0.00027[a]	0.00033±0.00038[a]	0.0654±0.0302

[a]Distances not significantly different from zero.

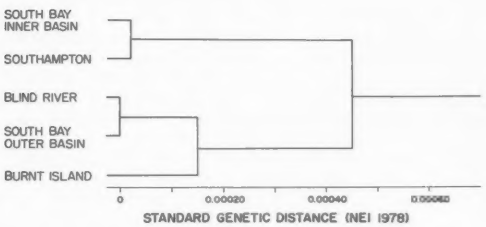


FIG. 6. Dendrogram produced by UPGMA cluster analysis of Nei's coefficients of genetic similarity for five whitefish stocks of Lake Huron. Nei's distances are based on electrophoretic data for 30 loci.

shore of Manitoulin Island. The morphometric, osseometric, and electrophoretic techniques did not show differences between these two stocks even though they were spatially discrete.

A similar study of this species in Lake Winnipeg (Kristofferson 1978) also found that morphological and electrophoretic characters could be used to distinguish one "subpopulation" from several others. However, the remaining subpopulations were uniform biochemically, but divisible into four groups morphologically.

In the present study, as well as that of Ihssen et al. (1981), the whitefish stock with the greatest degree of spatial and temporal isolation and slowest growth was most different for all characters including those associated with electrophoresis. Growth rate can influence morphological characters (Martin 1949; Todd and Smith 1980). The Inner Basin stock (*A*), which is much slower growing than other stocks in Lake Huron (Collins 1979), also was the most discrete morphologically and osseometrically. Some, but not all, of these differences may be attributed to this environmentally influenced feature.

The stock identification characteristics examined are expressions of genetic traits ranging from the polygenic to the single locus level, and could reflect features that are quite unrelated. It is apparent that spatially separated stocks within the same basin may share somewhat similar characteristics that collectively distinguish them from stocks in other basins.

Since most whitefish do not appear to migrate over great distances, each stock should be regarded as a functional unit for the purpose of fisheries management. The vital parameters that determine yield, assuming adequate recruitment of juveniles, are growth and mortality, two variables known to be strongly influenced by exploitation. A management strategy designed to maximize yield from an individual stock would not necessarily be appropriate to the management of a mixture of stocks, each growing at its own rate.

We conclude that the "stock concept" should be applied to the management of Lake Huron whitefish and that each stock represents a group of fish that is spatially separated and in varying degrees discrete, even though apparent differences may be influenced by environmental conditions. Since these spatially segregated stocks may be locally adapted in subtle ways, they should be managed to protect their integrity. Similar conclusions have been reached in other studies of the coregonines (Imhof et al. 1980; Todd and Smith 1980; Todd et al. 1981).

At the present time, tagging studies provide the best direct evidence of discreteness of these stocks. But morphometric and meristic, osseometric, and electrophoretic characters may provide additional understanding of the nature of that discreteness. These features can be used to identify changes in whitefish, so that unique characteristics can be recognized and, if necessary, protected.

Acknowledgments

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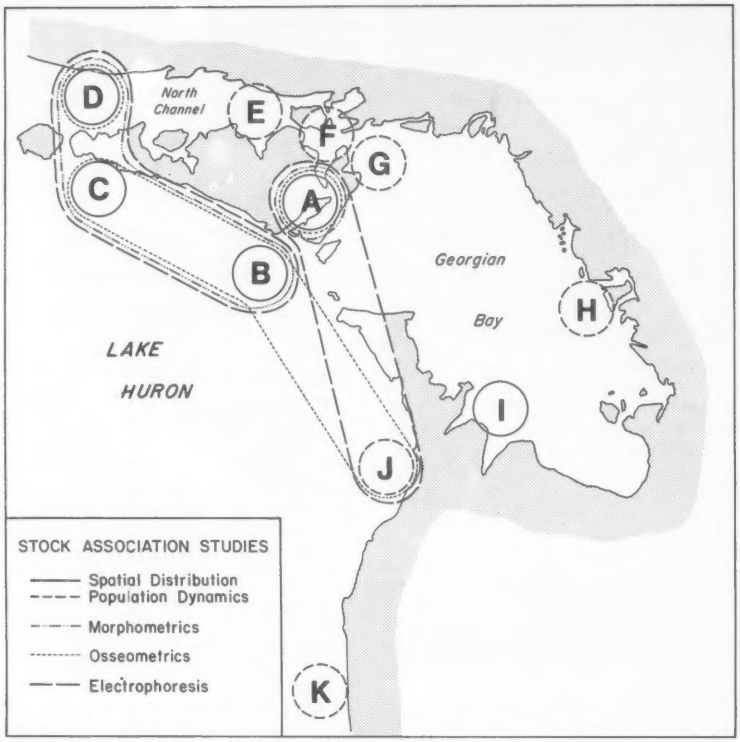

FIG. 7. Schematic presentation of the association among 11 stocks of whitefish of the Ontario waters of Lake Huron as determined by the four studies.

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Life History, Morphology, and Electrophoretic Characteristics of Five Allopatric Stocks of Lake Whitefish (*Coregonus clupeaformis*) in the Great Lakes Region[1,2]

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IHSSEN, P. E., D. O. EVANS, W. J. CHRISTIE, J. A. RECKAHN, AND R. L. DESJARDINE. 1981. Life history, morphology, and electrophoretic characteristics of five allopatric stocks of lake whitefish (*Coregonis clupeaformis*) in the Great Lakes region. Can. J. Fish. Aquat. Sci. 38: 1790 – 1807.

Ecological, morphological, and electrophoretic variation among five allopatric Ontario lake whitefish (*Coregonus clupeaformis*) stocks was studied. The stocks differ in terms of diet, growth rate, movement patterns, fecundity, and egg and larval size. Morphologically, the five stocks were also different for characters such as number of gill rakers, number of pyloric ceca, and in size, adjusted for fork length, of the tail, dorsal fin, and the eye. Discriminant functions, derived from body measurements and meristic counts, classified specimens accurately into their lakes of origin. Highly significant allele frequency differences were found at 6 of the 32 electrophoretic loci examined. Standard genetic distances, derived from electrophoretic allele frequency differences, corresponded roughly to the order in which these stocks became isolated following retreat of the last continental glaciation. The genetic distance of the Opeongo stock from the other stocks is about one order of magnitude larger than the genetic distances among the other stocks. The Opeongo stock is also somewhat unusual ecologically, having different egg size and fecundity characteristics compared with the other stocks and being a member of a sympatric dwarf/normal pair. Dendrograms, derived from the Mahanalobis distances for the meristic variation and the Nei genetic distances for the electrophoretic variation, showed similar branching patterns, but the branching patterns for the morphometric versus the biochemical variation were different. A significant part of the morphometric variation among the stocks was related to differences in growth rates of the stocks, most body measurements being negatively correlated with growth rate. The Mahanalobis distances for the meristic variation (including pyloric ceca counts) were correlated with the standard genetic distances from the electrophoretic data. The ecological, morphological, and biochemical variation among the stocks, in relation to local adaptation, is discussed.

Key words: lake whitefish, stock concept, genotype, phenotype, ecology, morphology, meristics, multivariate analysis, electrophoresis, growth, diet, fecundity

IHSSEN, P. E., D. O. EVANS, W. J. CHRISTIE, J. A. RECKAHN, AND R. L. DESJARDINE. 1981. Life history, morphology, and electrophoretic characteristics of five allopatric stocks of lake whitefish (*Coregonis clupeaformis*) in the Great Lakes region. Can. J. Fish. Aquat. Sci. 38: 1790 – 1807.

Nous avons étudié la variation écologique, morphologique et électrophorétique chez cinq stocks allopatriques de grands corégones (*Coregonus clupeaformis*) de l'Ontario. Les stocks

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diffèrent sous le rapport du régime alimentaire, du taux de croissance, des modalités de déplacement, de la fécondité et de la taille des œufs et des larves. Morphologiquement, les stocks diffèrent beaucoup également par des caractères tels que le nombre de branchicténies et de caeca pyloriques, et par la taille, ajustée en fonction de la longueur à la fourche, de la queue, de la nageoire dorsale et de l'œil. Il a été possible, à l'aide de fonctions discriminantes dérivées de mensurations du corps et de comptages méristiques, de classer avec grande précision les sujets selon leur lac d'origine. À 6 des 32 loci électrophorétiques examinés, nous avons trouvé des différences hautement significatives dans la fréquence des allèles. Les distances génétiques standard, déduites des différences de fréquence alléliques déterminées électrophorétiquement, correspondent en gros à l'ordre dans lequel ces stocks ont été isolés après le retrait de la dernière glaciation continentale. La distance génétique chez le stock d'Opeongo par rapport aux autres stocks est plus grande d'environ un ordre de grandeur que les distances génétiques observées parmi les autres stocks. Au point de vue écologique, le stock d'Opeongo est aussi quelque peu exceptionnel : la grosseur des œufs et les caractéristiques de fécondité diffèrent de celles des autres stocks, et ce stock est un membre d'une paire naine/normale sympatrique. Des dendrogrammes, dérivés des distances de Mahanalobis pour la variation méristique et des distances génétiques de Nei pour la variation électrophorétique, montrent des ramifications identiques, mais le schéma des ramifications dans le cas de la variation morphométrique versus variation biochimique est très différent. Une portion significative de la variation morphométrique entre les stocks a été reliée à des différences dans le taux de croissance des stocks, la plupart des mensurations du corps ayant une corrélation négative avec le taux de croissance. Nous avons trouvé une corrélation entre les distances de Mahanalobis pour la variation méristique (y compris les comptages de caeca pyloriques) et les distances génétiques standard dérivées des données électrophorétiques. Nous analysons la variation écologique, morphologique et biochimique parmi les stocks, en fonction de l'adaptation locale.

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In view of widespread degradation of natural aquatic environments, often with decline or extinction of fish stocks as defined by Larkin (1972), it has become important to evaluate the genetic and ecological diversity of fisheries resources. An initial step towards preservation of existing fisheries resources is documentation of their diversity. In this paper, we compare phenotypic, genetic, and ecological characteristics of five allopatric lake whitefish (*Coregonus clupeaformis*) populations in southern Ontario and discuss the findings within the framework of the stock concept (Ricker 1972; Loftus 1976).

Our approach has been to analyze morphological variation among the study populations in terms of electrophoretic protein characteristics, body proportions, and meristic structure, and to assemble available ecological information for each. The above approach involves three distinct levels of organization: the structural biochemical level, the organismic level (morphology, physiology, behavior), and the ecological level (environmental factors, species interactions). Each level is of fundamental importance in the characterization of stocks, especially in the case of coregonine fishes which show extreme environmental plasticity (e.g. Svärdson 1970, 1979).

Recently, electrophoresis has been used to study biochemical variation among allopatric and sympatric whitefish populations (Lindsey et al. 1970; Franzin and Clayton 1977; Kirkpatrick and Selander 1979; Kristofferson 1978; Imhoff et al. 1980) The biochemical approach is particularly powerful in that the observed phenotype, represented by movements of isozymes in an electric field, is largely independent of environmental influences (Allendorf and Utter 1979) and is directly representative of genotype.

The Study Lakes

The populations investigated are those residing in Lakes Ontario (eastern basin), Huron (South Bay, inner basin), Opeongo, Lavieille, and Simcoe (Fig. 1). Selection of the study lakes was based on their geographic locations, which reflect varying degrees of spatial and temporal separation, and on the amount of existing background ecological information on their lake whitefish populations. Research field stations have operated on Lakes Opeongo, Ontario (Bay of Quinte), and Huron (South Bay) since 1937, 1953, and 1947, respectively, and published accounts are available on the whitefish populations in each locale (Kennedy 1943; Christie 1963; Budd 1957; Reckahn 1970, respectively). Fisheries assessment monitoring has been undertaken on Lake Simcoe whitefish since 1961 and several management reports are available (e.g. Evans 1978). Lake Lavieille is the least well-known of the five study lakes, with no previous information available on its whitefish population. Lavieille is included as a near neighbor comparison with Lake Opeongo. Physical and chemical characteristics of the study lakes are given in Table 1.

The Geomorphological Setting

The present distribution of lake whitefish corresponds generally with the area covered by continental glaciers (Lindsey et al. 1970). It has been postulated that separate refugia for whitefish persisted for about 40 000 yr (Lindsey et al. 1970); then as the glaciers retreated 10 000 to 15 000 yr ago, lake whitefish, along with a community of "glacio-

FIG. 1. The Great Lakes region showing locations of the study lakes.

marine relicts'' in the Great Lakes area, re-invaded newly formed postglacial lakes.

Lake histories in the study area are directly related to events of the last major continental glaciation, the Wisconsin. Maximum advance of the Wisconsin stage glacier occurred about 17 000 yr B.P. (''before present'' refers to the year 1950). By 12 500 B.P., retreat of the continental glacier had opened lakes Algonquin in the Huron basin and Iroquois in the Ontario basin (Prest 1976). At that time, Lakes Huron and Simcoe were directly connected but Lakes Opeongo and Lavieille to the North remained glaciated (Dadswell 1974, map 15; Prest 1976, map 16f). Lake Algonquin drained via three outlets: the St. Clair River, the Kirkfield Outlet into glacial Lake Iroquois and thus into present day Lake Ontario, and the Fossmill Outlet located northwest of Lake Opeongo (Martin and Chapman 1965). Gene flow between whitefish in the Great Lakes waters, including Lake Simcoe, was possible at that time, but Lakes Opeongo and Lavieille had not yet been colonized.

Due to discharge of water via the Fossmill Outlet (and differential uplift of the earth's surface), Lake Algonquin levels had dropped sufficiently by 11 200 B.P. to become separated from Lake Simcoe (Prest 1976). During this period, the glacier apparently receded from the Madawaska Highlands area surrounding Lake Opeongo, but areas exceeding 381 m elevation, including Lakes Opeongo and Lavieille, were not inundated by Lake Algonquin (Martin and Chapman 1965). Thus, colonization of the higher elevation lakes by fishes apparently involved upstream movements, possibly during this period.

By 10 500 B.P., Lake Algonquin water level had fallen to form low-level Lake Stanley in the Huron basin and Lake Hough in the Georgian Bay basin. This isolated South Bay's inner basin from northern Lake Stanley. However, during the Nipissing phase of the Great Lakes (5000–6000 yr B.P.), water levels rose and Manitoulin Island and South Bay resubmerged. About 4000 yr ago, South Bay reemerged and present-day Lake Huron–Georgian Bay took form (Lewis 1969; Terasmae 1979). Lake Huron water levels have remained relatively stable at 177 m for the past 2500 yr (Hough 1963).

Materials and Methods

Sampling of fish for morphological and electrophoretic analyses was undertaken during October and November, 1979 and 1980, with the exception of one sample of Lake Lavieille whitefish which was collected during July 1980.

Spawning, Incubation, and Early Life History

With the exception of Lake Lavieille, observations of spawning, hatching, and larval biology span 1–15 yr, with the most complete information being available for Lake Simcoe and South Bay. Larval studies span 3-9 yr in Lakes Opeongo, Simcoe, and South Bay whereas the only information available for Lake Ontario is that of Hart (1930). Surface and bottom trawls have been employed to capture larvae and juveniles. Adults have been sampled using trap nets, primarily during the spawning period.

Fecundity

Fecundity estimates have been obtained from intact ovaries of fish sampled during late September to November. Fecun-

TABLE 1. Physical and chemical characteristics of the five study lakes.

Lake	Lat. Long.	Elevation (m)	Area (km^2)	Depth (m) $\bar{z}$	Depth (m) z max.	Secchi (m)	Chemical TDS	Chemical pH	Chemical Alkalinity[a] T.F.E.	Chemical Alkalinity[a] T.I.P.
Lavieille	45°51″ 78°14″	386	24		49	5.0	24	7.0	8.4	6.4
Opeongo	45°42′ 78°23′	403	52	15	49	5.5	35	6.8	7.2	5.2
Simcoe	44°25′ 79°20′	219	725	17	41	4.5	200	8.3	125	
Ontario	43°40° 78°00°	75	19 477	80	237	5.5	134	8.0	93	
Huron (South Bay)	45°35′ 82°10′	177	73	20	59	6.0	155	8.4	87	

[a]T.F.E. (total fixed end point); T.I.P. (total inflection point); in $mg \cdot L^{-1}$ $CaCO_3$.

TABLE 2. List of morphological measurements and meristic counts.[b]

Morphological measurements	Code	Meristic counts	Code
Total length	TL	Number of gill rakers	TGR
Fork length	FL	TGR + rudimentary gill rakers	TRGR
Standard length	SL	Pored lateral line scales	LLP
Head length	HL	LLP + unpored lateral line scales	LLT
Head depth	HD	Suprapelvic scales	SPS
Snout length	SNL	Oblique rows of scales	ORS
Interorbital width	IN	Pelvic rays (principal)	PLRA
Maxillary length	MXL	PLRA + rudiments	PLRU
Maxillary width	MXW	Pectoral rays (principal)	PERA
Orbit diameter	OD	PERA + rudiments	PERU
Pectoral fin length	PCL	Anal rays (principal)	ARA
Pelvic fin length	PVL	ARA + rudiments	ARU
Caudal peduncle depth	CPD	Dorsal rays (principal)	DRA
Dorsal fin length	DL	DRA + rudiments	DRU
Dorsal fin width	DW	Branchiostegal rays left	LTB
Anal fin length	AL	Branchiostegal rays right	RTB
Anal fin width	AW	Abdominal vertebrae	AVE
Caudal fin length	CFL	Caudal vertebrae	CVE
Gill-raker length	GRL	Hypural vertebrae	HVE
		Pyloric ceca[a]	PC

[a]Pyloric ceca counts are included with the meristics for convenience.
[b]For measuring and counting procedures see Casselman et al. (1981).

dity was estimated gravimetrically from counts of eggs in three to six replicate subsamples of 100–400 eggs per fish. Individual egg sizes were estimated by weighing samples of individual eggs or by weighing 100 body cavity eggs per fish or by dividing total egg weight by total egg count.

FEEDING

Diet analyses have been drawn from previous studies with the exception of Lake Ontario and South Bay samples. Composition of diets is reported in percentage volume estimated by visual inspection at low magnification. Mean particle sizes have been derived from mean body sizes of the various dietary items, as reported elsewhere and from original data. Caloric values of various dietary items have been obtained from Johnson and Brinkhurst (1971), Cummins and Wuycheck (1970), and Salonen et al. (1976).

GROWTH

Whitefish age assessments reported here are based on scale interpretation. The scale aging technique has been validated for lake whitefish (Van Oosten 1923), although resolution of this technique tends to decrease for older specimens (Ovchynnyk 1962; Ausen 1976) and considerable caution must be employed. Scale age assessment for the Lake Simcoe population, which has an age structure skewed towards older ages due to recruitment failure, has been confirmed by examination of museum specimens and tag recoveries (Evans 1978).

Comparisons of growth in length between the different whitefish populations are based on back-calculation of scales. Scale radii through the anterior medial axis were measured from enlarged projections (×52) of scale impressions on acetate slides. Back-calculated size at age 4 has been employed as an estimate of growth rate for individual fish to assess growth effects on morphology.

MOVEMENTS

An overview of movements of adult lake whitefish in Lakes Simcoe, Ontario, and South Bay is presented. Observations are based on tag–recapture data collected during the past 2 decades. Distribution information for larval whitefish is available for Lakes Simcoe, Opeongo, Ontario (Hart 1930), and South Bay (Reckahn 1970; Faber 1970).

MORPHOMETRICS AND MERISTICS

For a sample of 30 fish from each population, 20 counts (19 meristic counts plus number of pyloric ceca) and 19 morphological measurements were taken (Table 2). We have employed counts and measurements such as gill-raker number and eye diameter that have been commonly used to study morphological variation of coregonids (e.g. Svärdson 1979), as well as characters less frequently used such as pyloric ceca counts and dimensions of the maxillary.

Analysis of covariance was applied to study the effect of size, age, and growth rate on the counts and measurements. As growth rate early in life has been shown to affect the proportion of body measurements (Martin 1949; Svärdson 1970), back-calculated fork length at age 4 was used as an estimator of early growth rate. The morphological measurements were tested for allometry using the relation $M = a(\mathrm{FL})^b$ transformed to $\log M = \log a + b \log (\mathrm{FL})$, where M is the measurement and FL the fork length.

A stepwise discriminant function analysis (SDFA) (Klecka 1975) was applied separately to the counts and measurements and also to the two data sets combined. Because we were interested in differences in body shape rather than the actual size of body parts, the measurements were adjusted for differences in body length by the formula $M_c = M(\overline{\mathrm{FL}}/\mathrm{FL})^b$, where

M_c is the adjusted measurement, M the original measurement, FL the fork length, $\overline{FL}$ the overall mean fork length, and b the regression coefficient of log M on log FL within lakes obtained from the analyses of covariance. The square of the distances in discriminant space among population centroids (Mahalanobis distance) was used in an unweighted pair-group arithmetic average (UPGMA) cluster analysis (Sneath and Sokal 1973) to illustrate the relationships among populations.

The discriminant functions were used to classify the 150 fish in the sample using a "jackknife" classification (Lachenbruch and Mickey 1968). In this classification, the bias of having used the individual that is being tested in the derivation of the discriminant function is partially removed by recalculating the group means and cross products without the case being classified. However, some spurious classification will still remain because the case under consideration is used to calculate the covariance matrices. To test for the amount of spurious classification, the 150 fish were randomly assigned to the five lake categories and a SDFA performed.

Electrophoresis

The same 32 loci and 12 enzyme systems assayed by Casselman et al. (1981) were used in this study. Eleven of these loci were found to be polymorphic (*G3P-1*[3], *CPK-1*, *ME-2*, *IDH-3,4*, *LDH-2,3,4*, *MDH-3,4*, *PGM-2*). Of these polymorphic loci, only six were used in the subsequent analysis. Three polymorphic loci were considered monomorphic for the subsequent analyses because they involved only rare alleles (*CPK-1*, *LDH-3*(or 4)[4], *PGM-2*, $p < 0.01$), and two polymorphisms were not used because no satisfactory genetic model fitted the data (*ME-2*) or the electrophoretic results were not repeatable after frozen storage of the tissue (liver) samples (*IDH-3*). Genetic models for the remaining polymorphisms involving six loci have been previously described (*G3P-1*, Clayton et al. 1973; *MDH-3,4*, Franzin and Clayton 1977; *LDH-1,2*, Imhof et al. 1980; *LDH-3,4*, Clayton and Franzin 1970; *IDH-3,4*, J. W. Clayton, personal communication, and P. E. Ihssen, unpublished data) and were confirmed in our laboratory from breeding data.

Because some difficulty was experienced with the repeatability of the *IDH-3,4* liver polymorphism, a second sample of fresh livers from Lakes Lavieille and Opeongo was assayed from a collection of the 1980 fall spawning aggregation. Again, the *IDH-3* polymorphism gave inconsistent results but the results for the *IDH-4* polymorphism were repeatable.

The phenotypic proportions of the samples were tested for Hardy–Weinberg equilibrium using a maximum likelihood ratio test (Sokal and Rohlf 1969). *MDH-3,4*, for which the isozymes of the two loci could not be differentiated, was treated in the same way as in Casselman et al. (1981).

For each enzyme system, allelic and phenotypic proportions among samples were compared using χ^2 homogeneity tests based on maximum likelihood ratios (Sokal and Rohlf 1969). Standard genetic distances among populations and average heterozygosity per locus and their standard errors for each population were calculated using a computer program supplied by Nei (1978). To illustrate genetic relationships among the populations, UPGMA cluster analysis based on the standard genetic distances was used (Sneath and Sokal 1973).

Results

Life History Characteristics

Spawning, incubation, hatching, and larval characteristics — Spawning habitat varies markedly among the five study lakes, the nature of the substrates and number of available sites being the primary differences. Lake Opeongo is characterized by numerous narrow, shoreline ledges of broken granitic rock and several cobblestone shoals of a hectare or less in area. Lake Lavieille has a shoreline structure somewhat similar to Lake Opeongo but no information is available on whitefish spawning sites. Lake Simcoe has numerous expansive shoal areas of limestone boulders ranging in depth from 0 to 10 m. Of 12 shoal areas that have been surveyed by diving, the mean surface area from 0- to 8-m depth is about 100 ha, ranging from 6 to over 400 ha. In contrast with Lake Simcoe, South Bay has only four known whitefish spawning shoals, and of these, Golding Point in the northwest quadrant is the major site. The principal whitefish spawning area for eastern Lake Ontario was the Bay of Quinte. The Bay of Quinte contained three geographically discrete whitefish spawning populations, including the Trent River group, which is still active but small, Big Island near Belleville, and Hay Bay. In the 1960s, whitefish largely disappeared in the Bay of Quinte leaving the lakeshore of Prince Edward County as the only major whitefish spawning area. Spawning habitat in the Bay of Quinte consisted of restricted shoals of flattened limestone rocks (Hart 1930) whereas the lakeshore spawning grounds consist of an extensive shoreline of limestone shelves.

Information on timing of spawning, hatching, and larval characteristics is summarized in Table 3. Information is not available for Lake Lavieille. Timing of spawning is earliest in Lakes Opeongo and Ontario, at the ends of the latitudinal range of the present study, suggesting some independence of latitudinal temperature effects. However, within lakes spawning appears to be correlated with water temperature, being advanced in cool years.

Hatching of whitefish eggs occurs during April and May in the study lakes, following immediately after ice-out. Hatching is earliest in Lake Ontario and South Bay and latest in Lake Opeongo. Opeongo whitefish, with spawning advanced and hatching delayed relative to the other study lakes, have an incubation period which is 1–2 wk longer than in Lakes Simcoe, Ontario, and South Bay.

Sizes of newly hatched, yolk-sac larvae shown in Table 3 indicate that Lake Opeongo whitefish larvae are 1.5–2.0 mm shorter than those from Lakes Simcoe, Ontario, and South Bay. When Lakes Simcoe and Opeongo whitefish eggs were artificially fertilized and incubated under similar laboratory conditions, the resulting Lake Opeongo larvae were 1.8 mm shorter than the Lake Simcoe larvae.

Immediately following hatching, larval whitefish occupy surface waters and are vulnerable to surface trawls for 4–6 wk. Peak catches of larval whitefish in surface trawls occur during late April to mid-May in our study lakes.

[3]Corresponds to *G-3-PDH-b* (Clayton et al. 1973).

[4]For the rare *LDH-3,4* allele, we have not been able to determine whether it is at the *LDH-3* or *4* locus.

TABLE 3. Spawning, hatching, and early life history information for four lake whitefish populations.

Lake	Peak spawning		Incubation history			Hatching		Size of yolk-sac larvae			Period of peak larval abundance in surface waters	
	Date	Temp. (°C)	Type[a]	Duration (d)	Temp. (°C)	Date	Temp. (°C)	n	$\bar{x}$ (mm)	±SD	Date	Temp. (°C)
Opeongo	Oct. 31–Nov. 15	4–7	N	175	0.1–6.0	Apr. 30–May 15	4–6	41	11.5	0.8	May 10–20	6.5–9.5
			A	160	1.1–5.0	Apr. 23	3.2	80	12.1	0.8	—	—
Simcoe	Nov. 15–30	3–6	N	160	0.1–8.0	Apr. 20–May 10	4–8	60	13.7	0.6	Apr. 30–May 20	3.5–15.0
			A	153	1.1–5.0	Apr. 23	3.2	45	13.9	0.8	—	—
Ontario (Bay of Quinte)	Nov. 2–20	6–8	N	160	0.1–12.0	Apr. 10–30	4–12	15	12.5	0.6	Apr. 20–May 4	4.0–12.0
(Eastern Basin)	—	—	A	130	1.1–9.0	Mar. 25	2.0	40	14.0	0.5	—	—
Huron (South Bay)	Nov. 12–26	4–8	N	167	0.1–7.0	Apr. 10–May 15	4–7	40	13.8	0.6	Apr. 18–May 16	4.5–9.0
			A	126	1.0–8.0	Apr. 20	3.0	20	14.0	0.2	—	—

[a]Natural versus artificial incubation.

TABLE 4. Fecundity, gonadosomatic index, and egg size characteristics of four lake whitefish populations.

Lake	Date of sample	No. of fish	Fork length (mm) $\bar{x}$ ± SD (range)	n	Egg size[a] weight/egg: Wet $\bar{x}$ (±SD)	Egg size[a] weight/egg: Dry $\bar{x}$ (±SD)	Gonado[b] somatic index % $\bar{x}$ ± SD	Fecundity (eggs/fish)	Fecundity (eggs/kg)	Regression constants ($\log_{10}$ fecundity = $a + b \log_{10}$ FL.): a	b
Opeongo	Sep. 28–Nov. 9	57	277±25 (215–360)	13	5.09 (0.92)	1.94 (0.10)	12.95±2.35	7632	27460	−1.844	2.338
Simcoe[c]	Oct.–Nov.	64	415±62 (320–580)	37	8.58 (0.91)	2.79 (0.12)	13.69±3.57	17466	20092	−5.733	3.807
Ontario	Oct.–Nov.	21	449±43 (381–572)	16	8.64 (1.36)	—	14.65±2.84	27536	21897	−5.116	3.595
Huron (South Bay)	Oct.–Nov.	72	441±39 (377–564)	47	7.44 (1.69)	—	12.31±3.80	17188	16401	−9.400	5.148

[a]Smaller samples were used for egg size determinations; in milligrams.
[b]Ovary weight/body weight during mid-October to mid-November.
[c]Includes data from Semple (1968).

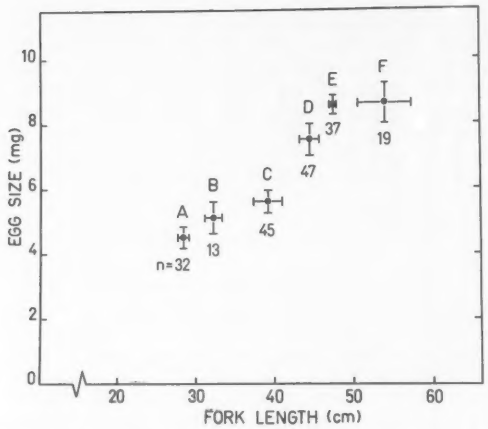

FIG. 2. Comparison of mean egg size versus mean fork length for four lake whitefish populations. Letters refer to: A, Lake Opeongo, 1976; B, Lake Opeongo, 1980; C, Lake Simcoe, 1966–67; D, South Bay (Lake Huron), 1947–73; E, Lake Simcoe, 1980; F, Lake Ontario, 1980. Numbers indicate sample sizes and ranges indicate ±2 SE.

Fecundity and egg size — Fecundity and egg size characteristics are summarized in Table 4. Lake Opeongo whitefish have less than one-half as many eggs per female as the other populations. However, on the basis of eggs per kilogram body weight, Lake Opeongo whitefish have 25% more eggs than the Lakes Simcoe, Ontario, or South Bay populations. Egg size is positively correlated with female body size among the study populations (Fig. 2). The Lake Opeongo whitefish egg is 40% and 27% smaller on the basis of wet and dry weights, respectively, than the Lake Simcoe egg (Table 4). A similar proportion of total metabolism appears to be channeled into egg production among the study populations as reflected by gonadosomatic indices of 12–15%. Small egg size, as in the Lake Opeongo population, for example, appears to compensate partially for maturation at a small body size. Hence, Lake Opeongo whitefish produce twice as many eggs at a fork length of 300 mm as would be expected for Lakes Simcoe or Ontario whitefish, if maturity were to occur at that size in the latter two populations (Fig. 3, Table 4).

Diet — Notable dietary differences occur among the study populations (Table 5). For example, amphipods and mysids (*Pontoporia* and *Mysis*, respectively) occur in major proportions in South Bay and Lake Ontario whitefish stomachs, respectively, whereas amphipods represent only 1% or less of the Lakes Opeongo and Simcoe whitefish diets, and mysids are completely absent. In Lakes Simcoe and Opeongo, reliance is much greater on zooplankton (12–39% by volume) and small mollusks (20–22% by volume). Among the study lakes, mean particle sizes consumed are significantly smaller, and the energy per unit weight of an average food particle less, for the Lakes Opeongo and Simcoe populations (Table 5). The populations utilizing the largest (Lake Ontario) and smallest (Lake Opeongo) mean food particle sizes in this study also have the fastest and slowest growth rates, respectively (Tables 5 and 7).

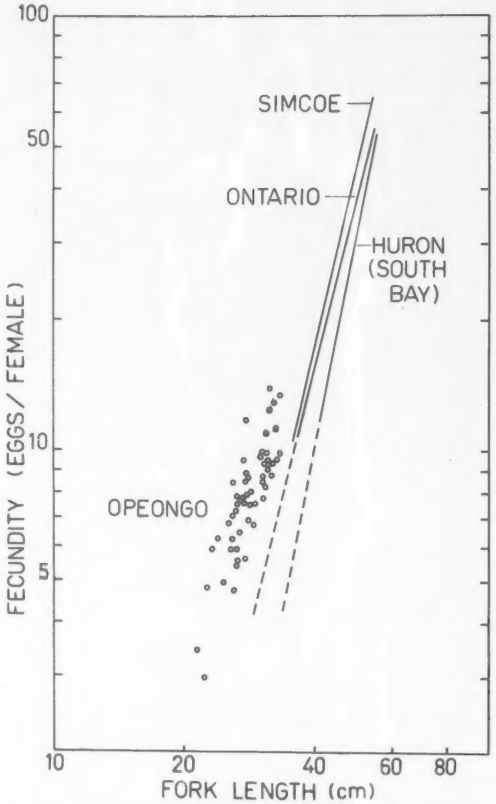

FIG. 3. Relationship between fork length and fecundity for four southern Ontario whitefish stocks. Circles represent individual whitefish from Lake Opeongo.

Growth — Mean ages, fork lengths, body weights, and length : weight regression constants are given in Table 6 for lake whitefish from each of the five study populations. These are the same specimens used for morphological comparison. Few individuals less than 9 yr of age are present in the Lake Simcoe population, as a result of recruitment failure during the 1970s (Evans 1978). Lake Simcoe whitefish are notably leaner than any of the other study populations (Table 6).

Growth rate varies widely among the populations, being highest in Lake Ontario, intermediate in South Bay and Lake Simcoe, and lowest in Lakes Opeongo and Lavieille (Fig. 4). Comparison of present estimates of growth rate in Lakes Opeongo, Simcoe, and South Bay with earlier studies on the same populations reveals close agreement (Table 7).

Distribution and movements — Larvae — In Lakes Op-

TABLE 5. Comparison of stomach contents during July and August of lake whitefish in four study lakes.

Dietary items	Diet characteristics: Particle size (mm) Length	Particle size (mm) Width	Energy[a] value g cal. · mg^{-1} dry weight	Stomach contents (% volume) Population: Ontario 1	Ontario 2	Huron (S. Bay)	Simcoe	Opeongo
Crustacea								
Copepoda	1.5	0.4	5.8	0.2	—	—	2.0	4.6
Cladocera	1.5	0.9	5.0	—	—	—	2.0	34.8
Ostracoda	1.5	0.8	5.6	—	—	0.1	8.0	—
Amphipoda	9.0	2.8	4.7	34.3	76.0	81.6	1.0	0.2
Mysidacea	15.0	4.0	5.6	53.8	—	—	—	—
Insecta								
Diptera	7.0	1.0	5.3	0.2	0.5	14.2	5.0	17.7
Ephemetoptera	8.0	2.5	5.5	—	—	0.1	18.0	2.7
Trichoptera	8.0	2.0	5.0	—	—	—	—	1.1
Other	7.7	2.0	5.2	—	—	—	1.0	1.8
Hydracarina	3.0	2.5	—	—	—	<0.1	4.0	6.0
Mollusca								
Pelecypoda	6.0	4.0	1.0	1.5	2.5	3.9	7.7	18.3
Gastropoda	6.0	4.0	—	9.9	—	—	14.3	1.6
Fish[b]	—	—	—	—	—	<0.1	3.0	11.0
Algae	—	—	—	—	—	—	8.0	—
Other plant material	—	—	—	—	—	—	3.0	—
Unidentified	—	—	—	—	21.0	—	22.0	—
No. of identifiable food items				6	3	9	10	10
No. of fish				16	15	6	30	280
Fish size (mm)				400–500		400–500	250–430	175–490
Source of data		Derived (see text)		1 Unpublished data 2 Hart 1931		Unpublished data	Hart 1931	Sandercock 1964

[a]Approximate values taken from the literature.
[b]Fish were considered to be incidental dietary items.

TABLE 6. Mean ages, fork lengths, and body weights for lake whitefish from each of five populations used in morphological and electrophoretic comparisons.

Lake of origin	n	Age (yr) $\bar{x}$	Age (yr) Range	Empirical values: Fork length $\bar{x} \pm$ SE (mm)	Empirical values: Body weight $\bar{x} \pm$ SE (g)	Regression constants ($\log_{10}$ Wt = $a + b \log_{10}$ FL) a	Regression constants b	Condition[a] coefficient K
Lavieille	30	9.4	4–15	324±5	440±22	−6.016	3.445	1.294
Opeongo	30	5.8	2–13	301±7	372±31	−5.511	3.237	1.364
Simcoe	30	14.1	9–21	489±4	1337±43	−4.158	2.707	1.143
Huron (South Bay)	30	9.3	4–14	411±7	942±69	−5.466	3.222	1.357
Ontario	30	7.7	2–14	528±15	1983±185	−6.394	3.534	1.347

[a]$K = (W/L^3) \times 10^5$, where W is the weight in grams and L is the length in millimetres.

eongo, Simcoe, Ontario, and South Bay, larval whitefish occupy surface waters for 1–1.5 mo after hatching (Table 3). In South Bay and the Bay of Quinte (eastern Lake Ontario), larvae appear to move or be displaced laterally in association with wind- or water-driven currents. In the Bay of Quinte, movement is from the western, upstream end to the eastern, downstream entrance to the Eastern Basin of Lake Ontario. In South Bay, newly hatched larvae become concentrated near shore in small coves at the north end of the bay, which receives the prevailing winds. In both South Bay and the Bay of Quinte, larval whitefish appear to move to the inshore zone where the cover of emergent vegetation is utilized (Hart 1930)

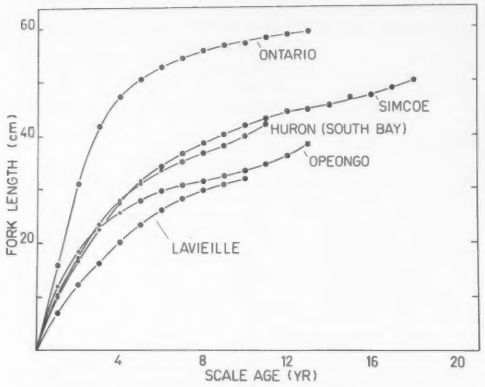

FIG. 4. Back-calculated growth curves for five southern Ontario whitefish stocks. Age interpretations based on scales.

and temperatures are warmest. In contrast with the above, whitefish larvae have been captured in Lake Simcoe at depths from a few metres to >10 m, 7–8 km offshore during the early limnetic stage (DesJardine 1979). In Lake Opeongo, whitefish fry have also been caught offshore in surface trawls over depths exceeding 20 m (D. O. Evans, unpublished data).

Comparative information on postlarval, juvenile behavior is lacking. However, Reckahn (1970) has successfully tracked the distribution of juvenile whitefish in South Bay and found a movement towards deeper water as the first summer progressed. Midsummer distribution was in association with the 17°C isotherm where it intersected the lake bottom. With the exception of a few samples collected by Hart (1930) in the Bay of Quinte, we are aware of no other observations on postlarval movements of lake whitefish.

Tagging studies done in Lakes Simcoe and Ontario suggest similar movement patterns for adult whitefish. The pattern which emerges is an annual movement towards a restricted home spawning zone of 10-20 km in breadth and a post-spawning movement to a more expansive feeding territory which may extend 50–80 km from the spawning (tagging) site (W. J. Christie, unpublished data; D. O. Evans, unpublished data). In both populations, mature whitefish frequently moved between shoals during the breeding period.

MORPHOMETRICS AND MERISTICS

The meristic counts (including pyloric ceca) were independent of fork length, with only 1 count out of 20 (anterior vertebrae) varying significantly with fork length at the 5% level. The five stocks were highly significantly different for most of the counts, with 14 counts with $P < 0.001$ and only 2 counts out of 20 nonsignificantly different among the five stocks at the 5% level (Table 8).

The analysis of covariance of the measurements on fork length and age showed that these covariates accounted for an average of about 80% of the variation within lakes. Regressing on log age after regressing on log fork length accounted for only an additional 3% reduction in the variation, on the average. Hence, the measurements were adjusted for fork length only and not age. The rate of change of each measurement with fork length was generally the same among the five lakes. Only 2 of the 18 measurements had regression coefficients significantly different among lakes at the 5% level. Hence, in the equation for the calculation of the adjusted measurements $M_c = M(\overline{FL}/FL)^b$, the pooled within-lakes regression coefficient was used for each measurement. The five stocks were highly significantly different for all morphological measurements, even after adjusting for differences in length (Table 9). These results are similar to those observed by Hart (1931) for whitefish, and reviewed for other species by Martin (1949) and, more recently, discussed by Svärdson (1970) for Scandinavian coregonids.

In the equation relating the measurement (M) to the fork length (FL), $M = a\mathrm{FL}^b$, some measurements had $b > 1$ (PCL, IN, MXW), referred to as positive allometry (Martin 1949), and some had $b < 1$ (CPD, OD, CFL, DL, DW, AL), referred to as negative allometry (Table 9). Generally, anteriorly in the head region the body parts increase proportionally with size ($b = 1$) or slightly faster ($b > 1$), except for the eye, and posteriorly they decrease proportionally with increase in size ($b < 1$).

The SDFA on the meristic counts gave highly significant differences among the centroids for the five stocks (approximate $F_{60,\ 154} = 11.9$, $P \ll 0.001$). Pairwise comparisons among the five stocks showed that all 10 comparisons were highly significantly different. All four canonical discriminant functions were highly significant accounting for 40, 35, 21, and 5% of the variability. The four counts giving the best discrimination among the stocks in order of their discriminating power were TGR, PC, AVE, and LLP. The values of the first two canonical discriminant functions, which account for 75% of the variability, were plotted for each fish (Fig. 5). The first function separated the Lake Opeongo stock from the other four stocks (Fig. 5), primarily on the basis of gill rakers and pyloric ceca. The Lake Opeongo fish had more gill rakers than the other four stocks and fewer pyloric ceca than the Lakes Ontario and Huron stocks (Table 8). The second canonical function separated the Lake Lavieille fish, primarily on the basis of lateral line scales. The Lake Lavieille fish had fewer scales than the other three populations. The jackknife classification categorized 115 of the 150 fish, or 77%, into their appropriate lakes of origin.

The SDFA on the adjusted body measurements (henceforth referred to as the body measurements) gave highly significant differences among the stock centroids ($P \ll 0.001$). As for the counts, all pairwise comparisons among the five stocks were highly significant. The first two canonical discriminant functions accounted for 69 and 17% of the variability, respectively (8 and 5% for the third and fourth functions, respectively), and their values for each fish were plotted (Fig. 5). The four measurements giving the best discrimination were SL, OD, IN, and DL, in order. The first function separated the Lake Ontario fish from the Lakes Opeongo and Lavieille fish (Fig. 5), primarily on the basis of dorsal fin length and standard length. The Lake Ontario fish had proportionally larger standard lengths (or shorter tails) than the Lakes Opeongo and Lavieille fish (Table 9). The jackknife classification categorized 121 of the 150 fish, or 81%, into

their correct lakes of origin. Combining the counts and measurements in one SDFA resulted in a jackknife classification of 140 of the 150 fish, or 93%, into their appropriate lakes of origin. The characters TGR, SL, PC, and MXL, in order, gave the best discrimination. The first two discriminant functions accounted for 75% of the variability and separated the scatter plots for the five stocks almost completely, with significant overlap only between the Lakes Simcoe and Huron stocks (Fig. 6).

Randomly assigning the 150 fish into five classes (lakes) and performing a SDFA on the counts and measurements resulted in a jackknife classification that allocated 36% of the fish correctly into their arbitrarily assigned classes, a somewhat higher correct classification than the 20% expected by chance. This result indicates that for relatively small numbers of individuals per class (30 in this example), even the jackknife classification produces some spurious correct classifications above that expected randomly.

To test the power of the discriminant functions for identifying fish from the different stocks, a second sample of one fish from each lake was collected in the fall of 1980, counted, measured, and classified by the discriminant functions developed from the completely independent 1979 (summer 1980 for Lake Lavieille stock) data. All five fish were correctly identified as to their lakes of origin by the discriminant functions (Fig. 6).

The dendrograms, derived by UPGMA cluster analysis from the Mahanalobis distances among the stocks, showed different relationships among the stocks for the meristic counts versus the morphological measurements (Fig. 7). For example, for the measurements the Lake Ontario fish are several branch points removed from the Lake Huron fish, but are closely associated with the Lake Huron stock for the meristic counts. Similarly, but to a lesser degree, the Lakes Opeongo and Lavieille fish are more closely associated for the measurements than for the counts.

The analysis of covariance of body measurements and counts on back-calculated fork length at age 4 showed that most of the body measurements varied significantly with this measure of early growth, whereas none of the counts did. The rate of change of the body measurements with back-calculated fork length at age 4 was not significantly different among the five stocks, with only 1 of 18 measurements (HL) having significantly different regression coefficients among the stocks at the 5% level.

Most measurements varied negatively with early growth and, hence, the faster growing fish have proportionally smaller body parts. The largest effect was on the characters SL, OD, HL, CFL, CPD, and MXL, with among-stock correlation coefficients between mean back-calculated fork length and mean body measurement of 0.98, −0.86, −0.90, −0.97, −0.83, and −0.87, respectively. Correcting the body measurements for among-stock variation in early growth reduces the variation among stocks for body measurements significantly, but does not eliminate stock differences. Sixteen of the 18 body measurements still have *F*-ratios significant at, at least, the 5% level. A discriminant function analysis on the body measurements adjusted for early growth differences among the stocks gave a correct jackknife classification into the five lakes of origin for only 59% of the

TABLE 7. Back-calculated fork lengths for lake whitefish from five study lakes.

Lake	*n*	Mean age (year-classes)	Scale age 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Reference
Lavieille	31	9.3	69	122	163	200	232	259	280	296	307	318	—	—	—	—	—	Present study
	(1966–75)																	
Opeongo	30	5.8	119	184	225	254	277	295	306	312	323	332	344	361	382	—	—	Present study
	(1966–77)																	
	140	6.2	108	162	208	247	288	329	265	296	426	465	483	—	—	—	—	Sandercock 1964
	(1953–61)																	
	399	5.8	110	148	177	210	236	245	269	296	353	404	—	—	—	—	—	Kennedy 1943
	(1929–35)																	
Simcoe	30	14.1	97	166	222	272	313	341	366	386	402	418	431	443	447	455	469	Present study
	(1958–70)																	
	598	8.1	98	165	220	253	326	340	349	363	384	391	406	427	457	481	519	Semple 1968[a]
	(1950–62)																	
Huron (South Bay)	30	9.3	103	173	233	277	308	334	349	366	380	398	421	443	528	536	—	Present study
	(1967–75)																	
	199		96	155	204	250	285	314	342	364	380	397	412	423	440	458	—	J. A. Reckahn, unpublished data
	(1931–39)																	
Ontario	30	7.7	159	309	417	473	504	526	543	557	567	570	581	586	592	—	—	Present study

[a]Ages from 1 to 4 only are back-calculated; other ages indicate empirical values for fall samples and are assumed to have completed growth to the year indicated.

TABLE 8. Summary of meristic counts (including pyloric ceca) (means with their standard errors). *, Significant at the 5% level; **, significant at the 1% level; NS, nonsignificant at the 5% level.

Count	Opeongo	Ontario	Simcoe	Huron	Lavieille	Total	$F_{4,145}$[a]	•
TGR	28.13±0.16	27.07±0.19	25.30±0.20	27.23±0.15	25.63±0.16	26.67±0.12	45.88	**
TRGR	28.37±0.18	27.37±0.22	25.80±0.18	27.40±0.16	26.47±0.18	27.08±0.11	27.69	**
LLP	82.03±0.67	83.77±0.60	85.40±0.47	86.23±0.59	80.83±0.56	83.65±0.30	15.11	**
LLT	82.87±0.63	84.83±0.60	85.93±0.50	87.50±0.60	82.87±0.56	84.80±0.30	11.92	**
SPS	8.43±0.12	8.33±0.10	8.43±0.09	8.60±0.11	8.17±0.11	8.39±0.06	3.16	*
ORS	10.00±0.10	9.83±0.08	10.10±0.11	10.13±0.10	9.37±0.09	9.89±0.05	10.33	**
PLRA	11.67±0.09	11.10±0.07	11.07±0.07	11.13±0.08	11.33±0.11	11.26±0.04	8.66	**
PLRU	13.67±0.09	13.07±0.08	13.07±0.07	13.13±0.08	13.33±0.11	13.25±0.04	8.74	**
PERA	15.80±0.13	15.53±0.12	15.53±0.13	15.37±0.12	15.73±0.16	15.59±0.06	1.67	NS
PERU	16.80±0.13	16.53±0.12	16.53±0.13	16.37±0.12	16.73±0.16	16.59±0.06	1.67	NS
ARA	12.03±0.14	11.33±0.13	11.20±0.10	11.33±0.12	11.27±0.13	11.43±0.06	7.51	**
ARU	14.93±0.15	14.27±0.14	14.07±0.13	14.30±0.13	14.20±0.14	14.35±0.07	5.95	**
DRA	11.60±0.12	10.90±0.10	10.87±0.09	10.97±0.11	11.47±0.12	11.16±0.06	9.68	**
DRU	14.47±0.13	13.97±0.16	13.70±0.11	14.00±0.14	14.27±0.16	14.08±0.07	4.27	**
LTB	8.37±0.09	8.97±0.11	8.87±0.11	8.90±0.10	8.83±0.07	8.79±0.05	5.92	**
RTB	8.23±0.09	8.67±0.10	8.47±0.10	8.70±0.09	8.67±0.10	8.55±0.04	4.22	**
AVE	39.47±0.18	39.20±0.23	39.77±0.19	40.10±0.19	37.93±0.17	39.29±0.11	18.30	**
CVE	16.73±0.11	17.20±0.16	16.83±0.11	17.37±0.17	17.17±0.13	17.06±0.06	3.76	**
HVE	4.43±0.18	3.93±0.05	3.93±0.05	3.97±0.03	4.00±0.00	4.05±0.04	5.86	**
PC	191.50±3.93	255.83±7.38	189.00±3.85	225.70±4.02	203.80±3.78	213.17±2.94	33.84	**

[a]*F* statistic from the analysis of variance for each count.

sample as compared with 81% when growth differences are included.

ELECTROPHORESIS

The phenotypic proportions for each sample and each locus or enzyme system did not differ significantly from Hardy–Weinberg equilibrium. Only 2 of 25 tests had χ^2 values larger than expected at the 5% level. A simultaneous χ^2 test (Cooper 1968) indicated that the magnitude of the two deviations found is expected at the 5% level for 25 independent tests. The Lake Simcoe sample had the largest χ^2 values, generally, suggesting that perhaps a slightly heterogeneous population was sampled. In general, these tests did not present any evidence that nonpanmictic populations were sampled (except perhaps Lake Simcoe), and also give further support to the genetic models for these enzyme systems tested previously by breeding experiments. Treating *MDH-3,4*, either by the use of gametic frequencies (discussed in Casselman et al. 1981) or as two loci with equal allelic frequencies, gave similar results.

The phenotypic and allelic frequencies for each enzyme system (Table 10) were highly significantly different for the five stocks sampled ($P < 0.005$ for *LDH-2*, *LDH-4*, *MDH-3,4*, *IDH-4*, $P < 0.025$ for *G3P-1*). For the second sample of livers collected in the fall of 1980 from the Lakes Opeongo and Lavieille stocks, the phenotypic and allelic frequencies did not differ from the earlier samples collected from these two stocks.

The allelic frequencies for all 32 loci examined (except *ME-2*, *IDH-3*), including the monomorphic loci, were used to calculate standard genetic distances among the stocks and average heterozygosity per locus and their standard errors (Nei 1978) (Table 11). The genetic distances are generally larger by about one order of magnitude than those observed for sympatric whitefish stocks of Lake Huron (Casselman et al. 1981). Nine of the 10 genetic distances among these stocks were significantly different from zero, with only the Lakes Ontario and Huron (South Bay) distance nonsignificant (Table 11). These results are similar to those observed by Kristofferson (1978) for allopatric and sympatric whitefish stocks of Manitoba, based on nine alleles at five loci. The genetic distances observed in that study ranged from 0 to 0.0298, compared with 0 to 0.0359 in this study (Table 11).

The range of average heterozygosity per locus, based on 30 loci (0.0449 to 0.0833, Table 11), was similar to that observed for sympatric whitefish stocks (Casselman et al. 1981; Kirkpatrick and Selander 1979). The Lake Opeongo stock had the lowest average heterozygosity per locus among the five stocks.

The dendrogram, generated from the standard genetic distances (Fig. 6), shows that the Lake Opeongo stock is genetically very different from each of the other four stocks. The Lakes Huron and Ontario stocks, which were not significantly different, were only slightly different from the Lake Simcoe stock. The Lavieille fish are genetically much closer to the Lakes Simcoe, Huron, and Ontario fish than the Lake Opeongo stock. The smaller genetic distances among the Lakes Ontario, Huron, Simcoe, and Lavieille stocks (0.00214 and 0.00451) are, nonetheless, about one order of magnitude larger than those found among sympatric whitefish stocks of Lake Huron (0.00021 to 0.00076, Casselman et al. 1981).

Discussion

Characteristics of a fish stock would appear to develop as a result of complex interaction between genetic (biochemical level), organismic (level of emergent morphology, physiology, and behavior), and ecological factors (Lindsey 1981; Clayton 1981), and to a significant degree are dependent on

historical circumstances (e.g. Franzin and Clayton 1977).

Organismic and Ecological Comparisons

Spawning and hatching dates are similar among the study populations, with the exception that Lake Opeongo, and possibly Lake Lavieille, whitefish spawn earlier and hatch 1–2 wk later than the other study populations. Latitudinal differences in thermal regimes would appear to explain largely the spawning and hatching time variation, suggesting conservatism rather than divergence. However, meristic characters are sensitive to environmental effects, primarily during the embryonic stages (Tåning 1952), and several meristic characters (LLP, LLT, PLRA, PLRU, DRA, DRU, HVE) are consistently displaced in Lakes Opeongo and Lavieille from those in Lakes Ontario, Simcoe, and South Bay, as would be expected if extended incubation was exerting an influence. Counts are lower for lateral line scales and higher for dorsal rays, pectoral rays, and hypural vertebrae in Lakes Opeongo and Lavieille. Except for hypural vertebrae, the displacements are in opposite directions to those caused by decreased temperature (and longer incubations) under laboratory conditions for other fish species (Tåning 1952; Blaxter 1969). These differences cannot be reconciled here, but we suggest that incubation effects may explain some of the meristic variation.

Growth rate varies widely among the study lakes. Opeongo whitefish utilize small food particles having low energy content per particle and, along with Lake Lavieille, have the slowest growth among the study populations. Lake Ontario whitefish, having the largest mean particle size and highest energy content per particle in their diet, have by far the fastest rate of growth. As energy used in locating, capturing, handling, and processing food is diverted from growth, quality of food may explain some of the growth variation among the study populations. Growth rate in turn has been found to strongly influence body proportion as discussed below.

Diet quality also appears to be related to the number of pyloric ceca, fish having diets with small mean particle size tending to have fewer ceca. Similar observations have been reported for other species (Svetovidov 1934; Reshetnikov 1961; DeGroot 1971). Function of the pyloric ceca is not well understood, although they are not thought to secrete digestive enzymes (Fänge and Grove 1979).

Relationship between gill-raker number or length and diet or feeding mode has frequently been reported (e.g. Svärdson 1952, 1970, 1979; Lindsey 1962; Loch 1974; Bodaly 1979), pelagic zone species and small food particle size generally being associated with high gill-raker counts or small gill-raker spaces (Kliewer 1970). Opeongo whitefish feed substantially on zooplankton and have the highest gill-raker count among our study populations. Lakes Lavieille and Simcoe whitefish have the lowest counts while Lake Ontario and South Bay are intermediate.

Lindsey (1981) suggests that presence or absence of related species influences the distribution of gill-raker number. He argues that gill rakers are sensitive to changes in the biological environment and, because of their key role in feeding, are probably subject to rigorous selection. Lindsey notes that gill-raker counts of lake whitefish tend to be lower if ciscoes

TABLE 9. Summary for the morphological measurements (means with their standard errors) adjusted for fork length (FL). $M_c = M(\overline{FL}/FL)^b$, where M_c is the adjusted measurement, M the original measurement, $\overline{FL}$ the overall mean fork length, and b the regression coefficient from the analysis of covariance. **, Significant at the 1% level; *, significant at the 5% level.

Measurement	Opeongo	Ontario	Simcoe	Huron	Lavieille	Total	$F_{4,145}$[a]		b[b]
TL	442.51±0.67	439.80±1.38	439.18±0.83	440.74±0.84	446.80±0.73	441.81±0.47	4.23	**	0.98[c]
SL	362.23±0.85	374.92±1.26	365.54±0.74	365.00±0.97	360.18±0.78	365.57±0.59	37.48	**	1.00[c]
HL	78.43±0.43	74.66±0.51	77.96±0.45	79.98±0.75	80.86±0.54	78.38±0.30	19.38	**	1.00[c]
HD	34.38±0.26	33.66±0.59	31.90±0.39	34.25±0.38	35.70±0.40	33.98±0.21	10.67	**	0.97[c]
SNL	19.24±0.22	18.62±0.25	19.72±0.22	20.30±0.28	19.72±0.31	19.52±0.12	5.82	**	1.09[c]
IN	23.53±0.32	21.95±0.26	21.18±0.22	23.08±0.29	22.17±0.19	22.38±0.13	12.75	**	1.21
MXL	21.11±0.26	19.24±0.28	20.54±0.22	21.63±0.23	22.29±0.23	20.96±0.14	22.62	**	0.95[c]
MXW	7.78±0.11	7.16±0.12	7.54±0.09	7.90±0.11	8.30±0.13	7.74±0.06	14.02	**	1.14
OD	19.11±0.14	18.17±0.15	19.54±0.13	19.03±0.17	20.51±0.18	19.27±0.09	30.16	**	0.80
PCL	63.57±0.80	61.08±0.69	63.18±0.51	63.28±0.78	68.71±0.62	63.96±0.37	17.37	**	1.08
PVL	54.52±0.41	57.20±0.53	59.69±0.45	57.36±0.68	57.38±0.64	56.63±0.26	4.77	**	0.84
CPD	29.70±0.19	28.27±0.29	29.17±0.25	30.17±0.27	30.47±0.21	29.56±0.13	12.63	**	0.82
DL	56.29±0.51	64.90±0.78	60.88±0.55	60.73±0.86	60.62±0.57	60.68±0.37	20.63	**	0.63
DW	44.93±0.55	42.40±0.62	39.97±0.48	42.78±0.63	44.27±0.51	42.87±0.28	11.93	**	0.89
AL	40.96±0.47	45.67±0.51	44.84±0.45	45.32±0.61	43.68±0.58	44.09±0.27	12.85	**	0.73
AW	41.88±0.51	39.66±0.43	37.61±0.56	41.34±0.48	43.59±0.50	40.82±0.28	21.14	**	1.00[c]
CFL	35.20±0.48	30.38±0.43	33.81±0.44	33.62±0.53	36.14±0.32	33.83±0.25	23.97	**	0.79
GRL	7.33±0.15	6.96±0.09	6.75±0.14	7.00±0.15	7.21±0.16	7.05±0.06	2.68	*	0.95[c]

[a] F statistic from the analyses of covariance for each measurement (covariate fork length).
[b] Pooled within lake log regression coefficient for each measurement.
[c] Not significantly different from 1.00.

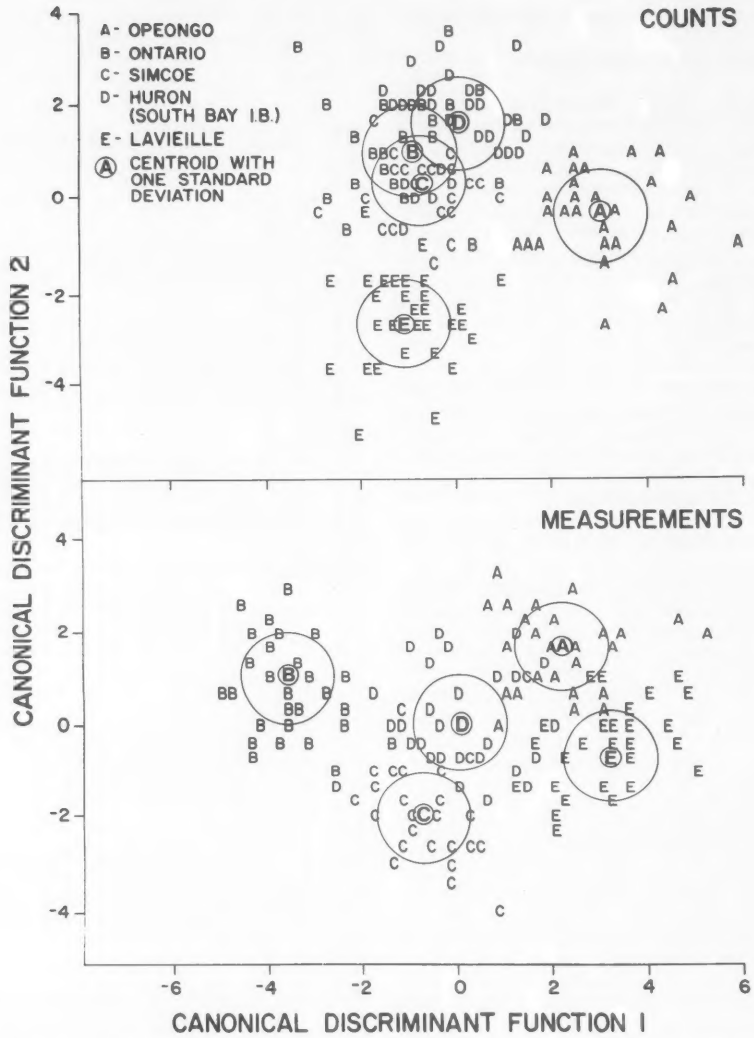

FIG. 5. Scatter plots derived from a stepwise discriminant function analysis on 19 meristic counts plus pyloric ceca counts and 18 morphological measurements for five southern Ontario whitefish stocks.

(*Coregonus artedi*) are present in the same lake, and that where morphologically divergent forms of the lake whitefish occur sympatrically, the smaller form (dwarf) usually has a higher gill-raker number than the normal (large) form. Lake Opeongo whitefish are unusual with reference to both points. Introduction of ciscoes in 1948 (Martin and Fry 1972) has not resulted in a decline in gill-raker number in the lake whitefish, as might be expected (Lindsey 1981), and normal and dwarf whitefish in Lake Opeongo have high (27.7 ± 0.2) and low (25.4 ± 0.1) gill-raker counts, respectively (Kennedy 1943). Opeongo dwarfs are notably benthic in orientation in contrast with the limnetic, high gill-raker forms found in Yukon lakes (Bodaly 1979; Lindsey 1962), which possibly explains their continued existence in Lake Opeongo following introduction of the ciscoe.

Fecundity, egg size, and larval size vary significantly among the study populations. Notably, Lake Opeongo whitefish have small eggs and larvae and high fecundity. Small egg

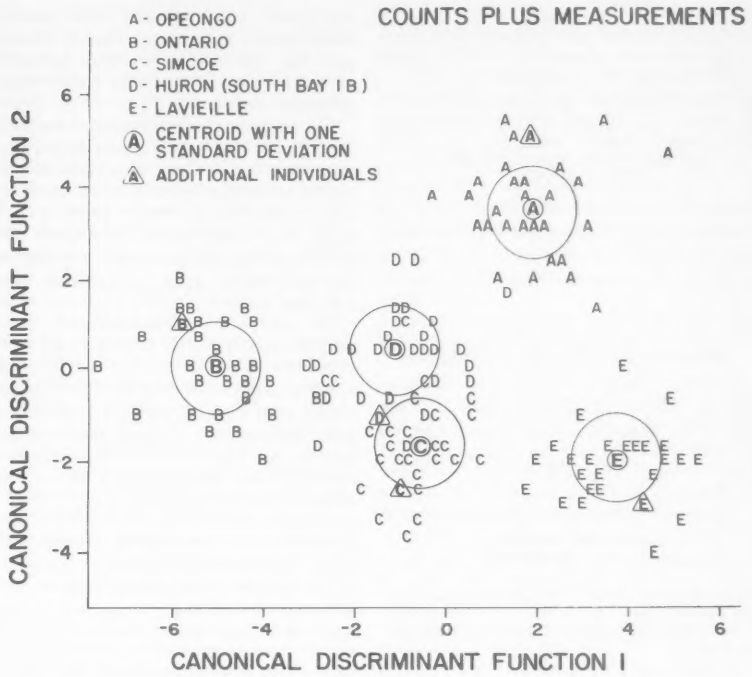

FIG. 6. Scatter plot derived from a stepwise discriminant function analysis on 38 morphological characters (counts and measurements) for five southern Ontario whitefish stocks.

size results in compensatory fecundity in populations with small body size, whereby a fixed proportion of total metabolism is directed to egg production, but increased numbers of eggs are produced at a given body size. For other species, small larvae have been reported to have lower rates of survival than larger larvae (Bagenal 1978), suggesting that early mortality rates may vary among our study populations according to egg and larval size.

Positive correlation between egg size and fish length has been reported for Atlantic salmon (*Salmo salar*), rainbow trout (*Salmo gairdneri*), and other species (Galkina 1970; Bagenal 1978), although the relationship between egg size and fecundity for fish of the same species and size from sympatric or allopatric stocks has rarely been reported. One exception concerns two allopatric whitefish populations that have a negatively correlated fecundity : egg size relationship (Bidgood 1974). The fecundity : fork length regressions for these populations have different slopes and intercepts, and the population with smaller mean body size produces larger eggs than the population of larger fish. This is reversed with reference to the present findings, indicating that egg size : fecundity relationships can show extreme variation.

Movements of adult lake whitefish in the study lakes suggest two potentially important behavioral phenomena related to the stock concept. First, in Lakes Simcoe and Ontario movements of adults during breeding and nonbreeding periods suggest that a home spawning range exists that is geographically more confined than the total territory frequented during other times of the year. Hence, sympatric stocks may co-inhabit an area for a major portion of the year but spawn at widely separated locations, as was the case in eastern Lake Ontario (Christie 1972) prior to the loss of the Bay of Quinte stock. Our observations suggest return to a spawning area of several kilometres in breadth, but do not enable us to address directly the question of natal or repeat homing to a specific shoal. The second point concerns observations of whitefish spawning sites in South Bay that indicate that certain sites along the southeastern shore, which were active spawning sites when population densities were high, have been abandoned as the population has declined. Whitefish spawning appears to be concentrated at the best available sites when densities are low. Whether this process involves annual selection of spawning sites, or repeat spawning with high quality shoals tending to recruit more adults at all levels of recruitment, is unknown.

ORGANISMIC AND GENETIC ASPECTS

The dendrograms for the electrophoretic and meristic variation (including pyloric ceca) have similar branching patterns whereas the dendrogram for the morphometric variation is very different (Fig. 7). The correlation coefficients between

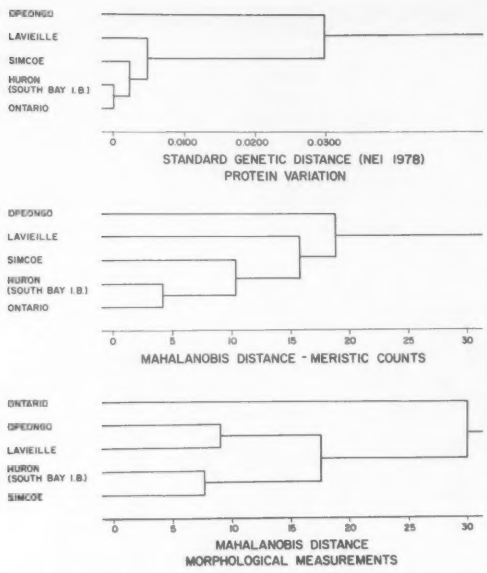

FIG. 7. Dendrograms produced by UPGMA cluster analysis of the Mahalanobis distances for the counts and measurements and the standard genetic distances for the electrophoretic data for five southern Ontario whitefish stocks.

the genetic distances, derived from the electrophoretic data and the Mahanalobis distances for the meristics and morphometrics, are 0.595 and 0.004, respectively, with the former significantly different from 0. These comparisons suggest that the meristic variation reflects the genetic relationships among the stocks more closely than the morphometric variation.

For the dendrogram derived from the body measurements, it was noted that stocks similar in growth rate are closely associated (Fig. 7). The Lakes Huron and Simcoe stock pair and the Lakes Opeongo and Lavieille pair, which have similar growth rates (Fig. 3), are also paired at the lowest branching points in the dendrogram. The Ontario stock, which is the fastest growing and not similar in growth rate to any of the other four stocks, appears on a separate branch at the highest branching point.

For multivariate comparisons of morphological measurement among closely related groups of organisms, it has sometimes been observed that the first canonical function, which accounts for most of the variability among the groups, reflects some simple biological variable such as growth rate or sexual dimorphism (e.g. Eyles and Blackith 1965; review by Blackith and Reyment 1971). In this study as well, a large portion of the morphometric (but not meristic) variation among stocks is probably due simply to differences in growth rates among the stocks. In the SDFA for the body measurements, it was noted that the coordinates for the five stocks of the first canonical function are strongly negatively correlated with the mean growth rates of the five stocks, as estimated by fork length at age 4 ($r = -0.92$). However, adjusting the body measurements for growth differences did not eliminate morphometric stock differences completely, and the resulting relationships among the stocks did not resemble the relationships obtained from the electrophoretic or meristic data. After adjusting for growth rate differences among

TABLE 10. Allelic frequencies for protein variants of five allopatric Ontario whitefish stocks.

	MDH-3,4[a]			*G3P-1*				*IDH-4*			*LDH-2*			*LDH-4*		
Stock	82[b]	100	*n*[c]	82	100	143	*n*	100	119	*n*	97	100	*n*	100	130	*n*
Lake Lavieille	0.456	0.544	45	0.359	0.337	0.304	46	0.488	0.512	85	0.011	0.989	46	1.000	0.000	46
Lake Ontario	0.340	0.660	36	0.317	0.550	0.133	36	0.706	0.294	34	0.111	0.889	36	0.972	0.028	36
Lake Opeongo	0.825	0.175	50	0.182	0.568	0.250	44	0.062	0.938	88	0.000	1.000	50	0.970	0.030	50
Lake Simcoe	0.352	0.648	86	0.308	0.465	0.227	86	0.671	0.329	41	0.064	0.936	86	0.680	0.320	86
Lake Huron (South Bay I.B.)	0.350	0.650	100	0.313	0.475	0.212	99	0.814	0.186	43	0.070	0.930	100	0.905	0.095	100

[a]Enzymatic nomenclature is according to Allendorf and Utter (1979).
[b]Allelic products designated by their mobilities relative to the bands reflecting the common allele designated as 100.
[c]Number of fish in the sample.

TABLE 11. Standard genetic distances and average heterozygocity per locus (Nei 1978) for five southern Ontario whitefish stocks. Genetic distances below diagonal, average heterozygosity on the diagonal.

Stock	Lavieille	Ontario	Opeongo	Simcoe	Huron (South Bay I.B.)
Lavieille	0.0734±0.0347				
Ontario	0.00341±0.00204	0.0735±0.0310			
Opeongo	0.01707±0.00930	0.03158±0.01900	0.0449±0.0233		
Simcoe	0.00554±0.00381	0.00243±0.00293	0.03254±0.01774	0.0855±0.0342	
Huron (South Bay I.B.)	0.00458±0.00338	0.00000±0.00029	0.03585±0.02262	0.00184±0.00180	0.0727±0.0307

stocks, the correlation between the Mahanalobis distances for the body measurements and the genetic distance increased from 0.004 to 0.285, but is still not significantly different from 0. Remaining environmental and genetic effects would appear to differentially influence the morphometric versus meristic characteristics.

Electrophoretic differences among stocks do not necessarily reflect recent local adaptation, but have been shown to be related to timing of geological events that have led to the founding of stocks. For example, Franzin and Clayton (1977) were able to relate allele frequency variation in whitefish stocks of western Canada to recolonization from glacial refugia of the Wisconsin glaciation. Also, ecological differentiation of stocks can occur with little electrophoretic differentiation. For example, Kirkpatrick and Selander (1979) have argued that speciation is occurring in sympatric stocks of whitefish in the Allegash Basin, with only minor changes in allelic frequencies as measured by electrophoresis. A dwarf form of the lake whitefish, reported to have a different rate of maturation and time of spawning, was electrophoretically similar to the normal form. Similarly, Allendorf et al. (1976) and Ryman et al. (1979) found two reproductively isolated sympatric stocks of brown trout (*Salmo trutta*) in a small Swedish lake that have different growth rates but are electrophoretically similar, although fixed for a different allele at the *LDH-1* locus. Perhaps these results should not be surprising as it has been convincingly argued (Wilson et al. 1977; Clayton 1981) that organismal and biochemical evolution are uncoupled and that biological differentiation may involve, for example, only regulatory genes rather than structural genes that have been extensively studied with electrophoretic techniques.

During the past 13 000–14 000 yr, our study area has been subjected to numerous shifts in lake levels as a result of glaciation (Robertson and Card 1972; Prest 1976). As the glacial front retreated, the lower study lakes (i.e. Lakes Ontario, Huron (South Bay), and Simcoe) were sequentially inundated by glacial lakes, colonized by whitefish and other species, and finally separated from one another as isostatic uplift and lowering of water levels occurred. Lakes Opeongo and Lavieille were not inundated by glacial lakes, but may have been flooded by proglacial lakes during periods of readvance of glacial ice (see Martin and Chapman 1965). Colonization of these lakes by highly motile species such as lake whitefish presumably occurred by upstream movement or intermittent passage via proglacial lakes. This hypothesis is suggested by the observation that neither Lakes Opeongo nor Lavieille contains the "glaciomarine" invertebrate fauna associated with nearby lakes at lower elevations adjacent to the Fossmill Outlet channel of glacial Lake Algonquin (Martin and Chapman 1965; Dadswell 1974).

Riverine connections between Lakes Huron and Simcoe and Lakes Huron and Ontario have persisted until the present time, although, due to distances and physical barriers between the basins, exchange of whitefish would seem improbable at present water levels (i.e. 2500 B.P. to the present, Hough 1963). Migration (gene flow) from Lake Huron to Lake Ontario via the Fossmill and North Bay outlets of glacial Lakes Algonquin and Nipissing, respectively, and the St. Lawrence River may have been possible until about 6000 B.P., although a brackish water link, the Champlain Sea, interrupted this connection from 11 200 to 8700 B.P. (Prest 1976, p. 719–722).

Impact of human fish-cultural activities during the 19th and 20th centuries, involving transplants of larval whitefish from Lake Huron to Lakes Ontario and Simcoe (Christie 1963; McCrimmon and Skobe 1970), is unknown. Success of larval plantings has generally been concluded to be low (e.g. Christie 1963), but some contribution to the recipient populations cannot be ruled out. In spite of the uncertainties of whitefish dispersal history in the study region, the pattern of genetic biochemical differences (Fig. 7) is generally consistent with the temporal and spatial pattern of separation among the lake basins.

Although the Opeongo fish fit into the general pattern of biochemical genetic distances and geological separation described above, the genetic distance of the Lake Opeongo stock to the other four stocks is unusually large (Fig. 6). The mean genetic distance among the stocks, excluding the Lake Opeongo stock, is about 0.003, whereas the mean of the Lake Opeongo stock to the other four stocks is about one order of magnitude larger (0.029). One possible explanation for this result is that the Lake Opeongo stock has gone through a bottleneck since its separation from the other stocks. If the stock was reduced to a relatively small number of individuals at the time of separation, or at some time after the separation from the other stocks, these individuals could have had unusual allelic frequencies due simply to sampling variation. In this regard it is interesting that the Lake Opeongo fish have the lowest level of heterozygosity per locus among the five stocks (Table 11). The other explanation, less likely in our opinion, is that the Lake Opeongo fish have gone through an unusually rapid, recent genetic change associated with local adaptation that is reflected in electrophoretic allele frequency differences.

A further observation, in light of the above result, is that the Lake Opeongo fish are also unusual meristically, having the largest Mahanalobis distances to the other stocks. They appear on a separate branch at the highest point in the dendrogram for the meristics. The Lake Opeongo fish are distinguished meristically by their smaller number of lateral line scales and pyloric ceca and larger number of gill rakers.

In addition to being segregated from the other stocks biochemically and meristically, there is an indication from the life history data that the Lake Opeongo fish are somewhat ecologically unique as well.

At present, it is unclear how to interpret the electrophoretic, morphological, and ecological findings in terms of localized ecological adaptation of stocks. In this study, the largest differences in life history strategy and meristic variation were associated with the largest electrophoretic differences. However, because this study involved only five stocks and the information on ecological differences among these stocks is incomplete, we are cautious about speculating on the generality of this observation. The possibility is not ruled out at present that the observed correlation between electrophoretic difference and meristic and ecological differences is simply due to chance. We believe, however, our data suggest that further investigations of within-species variation should involve biochemical and morphological, as well as ecological,

studies. Such an approach may lead to a better understanding of the local genetic adaptation of stocks, a problem that is of major concern to resource managers. In this regard a major shortcoming of present fisheries knowledge is the lack of detailed and precise life history information on fish stocks and its relationship to local genetic adaptation.

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Allelic Variability in Species and Stocks of Lake Superior Ciscoes (Coregoninae)[1,2]

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TODD, T. N. 1981. Allelic variability in species and stocks of Lake Superior ciscoes (Coregoninae). Can. J. Fish. Aquat. Sci. 38: 1808–1813.

Starch gel electrophoresis was used as a means of recognizing species and stocks in Lake Superior *Coregonus*. Allelic variability at isocitrate dehydrogenase and glycerol-3-phosphate dehydrogenase loci was recorded for samples of lake herring (*Coregonus artedii*), bloater (*C. hoyi*), kiyi (*C. kiyi*), and shortjaw cisco (*C. zenithicus*) from five Lake Superior localities. The observed frequencies of genotypes within each subsample did not differ significantly from those expected on the basis of random mating, and suggested that each subsample represented either a random sample from a larger randomly mating population or an independent and isolated subpopulation within which mating was random. Significant contingency χ^2 values for comparisons between both localities and species suggested that more than one randomly mating population occurred among the Lake Superior ciscoes, but did not reveal how many such populations there were. In contrast to the genetic results of this study, morphology seems to be a better descriptor of cisco stocks, and identification of cisco stocks and species will still have to be based on morphological criteria until more data are forthcoming. Where several species are sympatric, management should strive to preserve the least abundant. Failure to do so could result in the extinction or depletion of the rarer forms.

Key words: *Coregonus*, electrophoresis, genetic heterogeneity, speciation, Great Lakes

TODD, T. N. 1981. Allelic variability in species and stocks of Lake Superior ciscoes (Coregoninae). Can. J. Fish. Aquat. Sci. 38: 1808–1813.

On a fait appel à l'électrophorèse sur gel d'amidon comme moyen de reconnaître les espèces et les stocks du genre *Coregonus* du lac Supérieur. Sur des échantillons de cisco de lac (*Coregonus artedii*), de cisco de fumage (*C. hoyi*), de cisco kiyi (*C. kiyi*) et de cisco à mâchoires égales (*C. zenithicus*) provenant de cinq endroits du lac Supérieur, on a déterminé la variabilité allélique aux loci isocitrate déshydrogénase et glycérol-3-phosphate déshydrogénase. Les fréquences de génotypes observées dans chaque sous-échantillons ne diffèrent pas significativement de celles anticipées sur la base de croisements au hasard et laissent supposer que chaque sous-échantillon représente soit un échantillon aléatoire d'une population plus grande se croisant au hasard, soit une sous-population indépendante et isolée au sein de laquelle les croisements se font au hasard. Des valeurs significatives de carré de contingence pour des comparaisons à la fois entre localités et espèces suggèrent que parmi les ciscos du lac Supérieur il se trouve plus d'une population se croisant au hasard, sans toutefois révéler leur nombre. Par contraste avec les résultats génétiques de cette étude, la morphologie semble être un meilleur descripteur des stocks de ciscos, et l'identification des stocks et des espèces devra continuer à dépendre de critères morphologiques jusqu'à ce qu'on ait plus de données. Dans les cas où plusieurs espèces sont sympatriques, la gestion devrait s'efforcer de préserver la moins abondante. Autrement, il pourrait en résulter l'extinction ou la décimation des formes plus rares.

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DIVERSITY of morphology, ecology, genetics, and behavior in coregonine fishes is well known (Koelz 1929; Freidenfelt 1933; Steinmann 1950/51; Nikolsky and Reshetnikov 1970; Behnke 1972; Clark 1973; Ferguson 1974; White 1974; Ferguson et al. 1978; Rufli 1978; Kirkpatrick and Selander 1979; Svardson 1979; Todd and Smith 1980; Todd et al. 1981). The coregonine fishes of larger lakes, in particular, are generally subdivided into populations that appear to be independent of one another. In the most complex of such situations, as in the Great Lakes, for example, discrete populations exist both at the species and infraspecies levels. Research based on morphological and meristic characteristics

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has demonstrated the existence of several distinctive infraspecific populations of Great Lakes ciscoes, primarily of Lake Superior shortjaw cisco, *Coregonus zenithicus* (Todd and Smith 1980), but also of Lake Michigan bloater, *C. hoyi*, and *C. zenithicus* (T. N. Todd and S. H. Smith, unpublished data). Mayr (1969), in discussing the biological concept of the species, stated that "species are groups of interbreeding natural populations that are reproductively isolated from other such groups." However, virtually nothing is known about the reproductive isolation of coregonine populations, and hybridization seems to occur frequently and (as judged from experimental data) easily (Koelz 1929; Kajosaari 1957; Gasowska 1958; Garside and Christie 1962; Smith 1964; Svardson 1957, 1958, 1970, 1979; Pethon 1974; T. N. Todd unpublished data). An apparent lack of reproductive isolation suggests that the species of *Coregonus* rank as no more than semispecies (Svardson 1979). For practical purposes, however, populations of morphologically, ecologically, and genetically similar forms are grouped together and recognized as species by most workers on Great Lakes fishes.

Forms which are recognized are frequently found to consist of more than one population (Koelz 1929; Clarke 1973; R. Eshenroder, Great Lakes Fishery Commission, 1974, personal communication; Svardson 1979; Todd and Smith 1980). Each of these populations is considered to be a stock and therefore stocks of a species should be more similar to one another than to stocks of other species. However, environmental modification of phenotype during development in coregonines can make stocks appear more distinct than they really are genetically (Hile 1937; Svardson 1950; Clarke 1973; Loch 1974; Todd et al. 1981). Some stocks of lake herring (*C. artedii*), bloater (*C. hoyi*), and kiyi (*C. kiyi*) in Lake Superior are morphologically similar, and this similarity could be the result of a complex interaction of different genotypes and environment during development. Morphology, alone, leaves one unsure about the strength of conclusions concerning stock or species identification, but information on genetic similarities could clarify the relationships of stocks and species.

Richard Koehn (State University of New York, Stony Brook), who analyzed 200 ciscoes for the Great Lakes Fishery Laboratory in 1973, identified two enzymes with polymorphic loci — isocitrate dehydrogenase (EC 1.1.1.42) and glycerol-3-phosphate dehydrogenase (EC 1.1.1.8). Such polymorphic loci have been useful in examining relationships between species and stocks in many species of fish (Allendorf and Utter 1979). In the present study I used allelic variability of isocitrate dehydrogenase (IDH) and glycerol-3-phosphate dehydrogenase (G3PDH) to examine the genetic relationships of four species of Lake Superior ciscoes (*C. artedii*, *C. hoyi*, *C. kiyi*, and *C. zenithicus*), and several of their suspected stocks.

Sampling

A total of 535 ciscoes of the species *C. artedii*, *C. hoyi*, *C. kiyi*, and *C. zenithicus* were collected from commercial gillnet fishermen at five Michigan localities in Lake Superior (Fig. 1). The localities (labeled by commercial fishing grid numbers) and dates of collection were grid 1020, 32 km northwest of Keweenaw Peninsula portage channel, 110–128 m, May 23 1978; grid 1021, 24 km northwest of Keweenaw Peninsula portage channel, 165 m, May 23 1978; grid 927, 16 km northeast of Copper Harbor, 143–156 m, December 3 1978; grid 1029, 35 km east of Copper Harbor, 183–192 m, May 20 1978; grid 1429, 25 km north of Marquette, 119–128 m, December 7 1978. Only those fish which were alive at the time of net lifting were taken for analysis. This unfortunately resulted in some small collections because additional samples at each locality were not obtainable during the study period. All sample units containing less than 10 fish were excluded from the analyses. Potential genetic structuring was analyzed within and between the five localities and the four species.

FIG. 1. The five localities (labeled by the commercial fishing grid in which they occur) where ciscoes were collected in Michigan waters of Lake Superior.

The fish were frozen and taken to the laboratory where I used horizontal starch gel electrophoresis on muscle tissue to examine patterns of genetic variability at loci encoding for IDH and G3PDH. A small plug of white muscle was homogenized in an equal volume of distilled water with 300 mg/L nicotinamide adenine dinucleotide (NAD) and 200 mg/L nicotinamide adenine dinucleotide phosphate (NADP), and then centrifuged at 27 000 *g* for 30 min at 4°C. Electrode buffer was 0.04 mol/L citric acid adjusted to pH 6.9 with *N*-(3-aminopropyl)-diethanolamine, and gel buffer was a 1:5 dilution of this electrode buffer (after Clayton and Tretiak 1972). Gels consisted of Electro-starch and Connaught starch (3:1 ratio) in an 11% solution of buffer. Both NAD and NADP were added to gels and electrode buffers to a concentration of 100 and 40 mg/L, respectively. Supernatant from the centrifuged homogenates was inserted into the gels on small pieces (3 × 8 mm) of filter paper (Whatman no. 3). The filter paper inserts were removed after the electric current had been applied for about 30 min. Electrophoresis was conducted at 7.7 V/cm for about 18 h (overnight) at 4°C. Staining was modified from Shaw and Prasad (1970), mostly by the substitution of 3-(4,5-dimethyl thiazolyl-2)-2,5-diphenyl tetrazolium bromide for nitro blue tetrazolium.

Both IDH and G3PDH are encoded by two loci in coregonine white muscle. The locus labeled as 1 (the least anodal locus) was selected for each enzyme because of the low frequencies of variant alleles at the other locus. Similarly, phenotypes of alleles 180 (B^2) and 340 (B^3) at G3PDH were combined because of their low frequencies. The interpretation of the banding patterns on the gels followed Clayton et al. (1973) for G3PDH, and I am indebted to James Clayton

(Freshwater Institute, Winnipeg, Manitoba) for providing me with an unpublished interpretation of banding patterns for IDH. The nomenclature used is that suggested by Allendorf and Utter (1979).

Data Analysis

For each species at each locality, observed genotype frequencies were determined and compared with frequencies expected under conditions of random mating. The comparisons were tested by $\chi^2 = F_i^2 N$ where $F_i = 1 - H_i$ observed/H_i expected (H_i being the proportion of heterozygotes) and N denotes sample size (Workman 1969). The significance of heterogeneity in observed genotype frequencies was tested by contingency χ^2, which can be shown to equal $\chi^2 = \sum \left| \frac{a_i^2}{p_i q_i n} \right| - n$ where a_i is each observed value in each cell on the contingency table, $p_i q_i$ is the expected proportion for the ith cell based on marginal proportions, and n is the total number of observations (Spiess 1977). Comparisons between localities or species were done by pooling observations within each locality or species. Significant heterogeneity can occur as a result of stochastic processes as well as of heterogeneous selection.

Random Mating Expectations

The observed frequencies of genotypes within each subsample did not differ significantly from those expected on the basis of random mating, except in the single sample of *C. zenithicus* at G3PDH. Agreement of 27 of the 28 comparisons with Castle–Hardy–Weinberg expectations indicates that each sample of the species collected represents either a random sample from a larger random mating population, or an independent and isolated subpopulation within which mating is random.

Comparisons of Ciscoes from Different Localities

Little heterogeneity in allele frequencies existed among ciscoes within the localities sampled. (Raw allele frequencies for the 14 subsamples are given in Table 1.) Significant heterogeneity was not found within any locality (Table 2). However, the significant contingency χ^2 value ($P = 0.001$) for the observed genotype frequencies at G3PDH between localities suggested that more than one randomly mating population occurred among the five localities, but the general lack of genetic heterogeneity did not reveal how many such populations might be represented among the samples.

Species Comparisons

Genetic variability within and between the species was almost identical with that within and between the localities. Only within the four samples of *C. hoyi* were genotypic differences significant ($P = 0.050$), and then only at G3PDH-1 (Table 3). Comparisons between the species revealed significant heterogeneity at G3PDH ($P = 0.028$) and suggested, as did the locality comparisons, that more than one randomly mating population was represented in the samples.

More data, especially from some as yet undiscovered polymorphic loci, and larger sample sizes are necessary before the important taxonomic questions about the cisco species can be adequately addressed using genetic data. Based on the genetic data presented here, I calculate that detecting genetic differences of such small magnitude with 90% certainty at the 5% level of significance would require about 500 fish per sample unit (Sokal and Rohlf 1969).

TABLE 1. Frequencies of common alleles at two polymorphic loci in *Coregonus* (sample sizes in parentheses).

Locality[a] and nominal species	Allele frequency	
	IDH-1	G3PDH-1
Grid 1020		
C. artedii	0.59 (17)	0.85 (23)
C. hoyi	0.57 (52)	0.72 (63)
C. kiyi	0.61 (14)	0.76 (17)
C. zenithicus	0.68 (42)	0.74 (59)
Grid 1021		
C. artedii	0.60 (10)	0.82 (14)
C. hoyi	0.76 (12)	0.68 (17)
C. kiyi	0.75 (30)	0.83 (42)
Grid 1029		
C. hoyi	0.65 (13)	0.82 (17)
C. kiyi	0.74 (49)	0.82 (76)
Grid 927		
C. artedii	0.63 (41)	0.87 (45)
C. hoyi	0.76 (17)	0.89 (22)
C. kiyi	0.75 (59)	0.84 (69)
Grid 1429		
C. artedii	0.43 (14)	0.71 (14)
C. kiyi	0.65 (53)	0.82 (54)

[a]See Fig. 1 for location of grids.

TABLE 2. Genotypic heterogeneity of *Coregonus* within and between localities in Lake Superior.

Locality[a]	IDH-1			G3PDH-1		
	Cont. χ^2	df	P[b]	Cont. χ^2	df	P
Within						
1020	4.52	6	n.s.	6.89	6	n.s.
1021	4.91	4	n.s.	3.36	4	n.s.
1029	1.09	2	n.s.	0.004	1	n.s.
927	4.48	4	n.s.	0.96	4	n.s.
1429	4.50	2	n.s.	4.51	2	n.s.
Between	12.80	8	n.s.	26.23	8	0.001

[a]See Fig. 1 for location of grids.
[b]n.s. = not significant ($P > 0.05$).

TABLE 3. Genotypic heterogeneity within and between species of *Coregonus* in Lake Superior.

Species	IDH-1			G3PDH-1		
	Cont. χ^2	df	P	Cont. χ^2	df	P
Within						
C. artedii	4.34	6	n.s.	8.59	6	n.s.
C. hoyi	8.78	6	n.s.	12.61	6	0.050
C. kiyi	6.59	8	n.s.	8.01	8	n.s.
Between	10.60	6	n.s.	14.20	6	0.028

Existence of Stocks

Phenotypic diversity in Lake Superior ciscoes seems to have occurred without much genetic differentiation. Indeed, genetic variability in general is low in these fishes. A previous survey of enzyme variability in Lake Superior ciscoes gave a mean heterozygosity of 4.2%, with 7.9% of the 38 loci being polymorphic (unpublished data). Kirkpatrick and Selander (1979) showed some populations of lake whitefish (*C. clupeaformis*) to be polymorphic at 22−28% of examined loci, with an average heterozygosity of 6.8%, and Vuorinen and Lankinen (1978) found allopatric populations of *C. albula* in Finland to be polymorphic at 40% of examined loci with an average heterozygosity of 10%. Salmonids, as a whole, seem to be polymorphic at 10−51% of examined loci, with average heterozygosities of 1.5−13.9% (Gall et al. 1976; Allendorf and Utter 1979; Busack et al. 1979; Lynch and Vyse 1979). Lake Superior ciscoes appear to have fewer polymorphic loci than do other salmonids and the polymorphisms that do exist tend to be dominated by one or very few alleles. Populations of lake trout (*Salvelinus namaycush*) in Lake Superior also exhibited remarkably little genetic variability; polymorphisms occurred at only 7.7% of examined loci and average heterozygosity was 1.4% (Dehring et al. 1981). The low level of genetic variability makes detection of differences difficult.

Morphology seems to be better than genotype as a descriptor of cisco stocks. As previously mentioned, morphological characteristics were sufficient to resolve stocks of *C. zenithicus* in Lake Superior (Todd and Smith 1980). If the low estimates of genetic variability in the sampled loci are representative of the entire genome, the morphological differences between the stocks are probably the result of the influence of local environmental differences.

The existence of stocks as revealed by morphological studies is supported on a general level by the genetic data reported here. Significant genotypic differences between localities (Table 2) and between species (Table 3) revealed the probable existence of more than one population of ciscoes in Lake Superior. However, the taxonomic validity of the species of ciscoes is not resolved by this study. Until more data are forthcoming, identification of stocks and species will still have to be based on morphological criteria.

Formation of Stocks

The geographic location of a stock seems to be the most important factor in its formation. This is the site to which the fish may home, and hence is the source of the selective pressures that result in local genotypic and phenotypic adaptations. Environmental conditions at each locality also affect the development of the phenotype (Hile 1937; Svardson 1950; Clarke 1973; Loch 1974; Todd et al. 1981). The morphological distinctness of ciscoes from different localities as revealed in previous studies, compared with the general lack of observed genetic differences revealed in this study, suggest that the ciscoes of Lake Superior displayed more phenotypic responses to local environments than they did innate genetic differences.

The formation of stocks with phenotypic differences is probably a rapid process. The fish fauna of Lake Superior is only about 10 000 yr old (Dorr and Eschman 1970). However, the accumulation of genetic differences appears to be a slower process, as the stocks exhibit little genetic variability.

Evidence suggesting homing in coregonines is increasing (Lindstrom 1970; Clarke 1973; Imhof 1977; Leary 1979; Svardson 1979), and this behavior corresponds with the well-documented homing behavior of other salmonids. Homing would minimize gene exchange between stocks, and local selection pressures could modify the genome. Unfortunately, little is known about how precise homing is in whitefishes, or about how much gene flow occurs between adjacent stocks.

Differences in spawning time are an obvious mechanism for maintaining stock integrities. However, little is known about the ways such differences evolve. Certainly, slight differences of a few weeks magnitude could occur because of differences in environmental conditions at various localities, but differences as great as 6 mo in some stocks of *C. zenithicus* and *C. artedii* in Lake Superior (Todd and Smith 1980; T. N. Todd unpublished data) and shortnose cisco (*C. reighardi*) in Lake Michigan (Smith 1964) are more difficult to explain. Svardson (1979) described a new species, *Coregonus trybomi*, primarily because of its non-overlapping reproduction with *C. albula*. *Coregonus trybomi* may be polyphyletic, as may also be sympatric forms of *C. clupeaformis* (Lindsey et al. 1970; Kirkpatrick and Selander 1979). Because the reasons for differences in spawning time are not known, and because such differences may occur independently and repeatedly in coregonines, it is inadvisable to recognize species solely on the basis of spawning time. Examples of infraspecific groupings of salmonids with distinct spawning times are both numerous and well known (e.g. summer- and fall-run stocks of rainbow trout (*Salmo gairdneri*) and even- and odd-year spawning stocks of pink salmon (*Oncorhynchus gorbuscha*)). Spawning time may be similar to geographic isolation in its role in coregonine differentiation because morphological differences between stocks of *C. zenithicus* divided by spawning time were no greater than the differences between stocks divided by geographic distance (Todd and Smith 1980).

Management Implications

Earlier morphological studies, generally supported by the findings in the present study of biochemical genetics, have shown cisco populations in Lake Superior to be composed of locally adapted stocks. Ideally, management of the fisheries on ciscoes should take into account the existence of these stocks, to avoid the obviously detrimental effects of successively fishing to depletion one stock after another (Koelz 1929; Van Oosten 1929; Smith 1970; R. Eshenroder unpublished data; J. H. Selgeby U.S. Fish and Wildlife Service, Great Lakes Fishery Laboratory, 1980, unpublished manuscript). Where stocks of several species are sympatric, the relatively unselective (i.e. between different ciscoes of nearly the same size) gillnet fishery could seriously deplete or perhaps even extirpate the local stocks of the less-abundant species while the more abundant species might hardly be depressed. Genetic diversity is generally considered to be healthy and desirable for populations, and the existence of several species of ciscoes in a lake can likewise be considered as a healthy and desirable condition for the Great Lakes. The ideal management strategy for retaining this diversity in cisco

species would be to regulate the commercial catch within definable geographic areas so that stocks of the least abundant species in each area do not fall below predetermined levels of abundance. This strategy could be successfully implemented if managers knew the critical lower limits of population size and had the field capability of delimiting and estimating the actual size of each extant stock. However, much more needs to be known about the geographic boundaries of individual stocks before it is practical to manage them on such a sophisticated basis. Broad overlap in the distributions of some of the stocks, as well as species, of ciscoes and the difficulty of readily identifying various forms in the field add to the problems faced in the management and preservation of diversity in ciscoes.

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Variation among Stocks of Walleye (*Stizostedion vitreum vitreum*): Management Implications [1,2]

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Identification of races, strains, or subpopulations of walleye (*Stizostedion vitreum vitreum*) by examining differences in the morphology or biochemistry has met with relatively limited success. Although there is some genotypic evidence for stock discreteness, most evidence points to differences (age, growth, fecundity, maturity) which are believed to be phenotypic expressions induced by the environment. Thus, in the absence of clear genetic evidence, the biological differences are the reliable means of identifying and managing walleye stocks.

Walleye populations are spatially distinct, varying greatly in their rate of growth, rate of maturity, and longevity throughout their distributional range. Any genotypic expression of these population characteristics would probably be masked by environmental influences. There is no concrete evidence that differences in growth, age to maturity, fecundity, and longevity among walleyes are inheritable. The possibility of southern walleye populations being obligative riverine spawners suggests genetic differences, but this needs to be substantiated.

Some of the physiological variables used to delineate the responses of stocks to their environment can be useful as management tools to measure their responses to various disturbances, for example, exploitation and habitat modification. Measurement of specific fecundity indicates the relative ability of species to replace themselves. Measurements of mean age of the catch and age of onset of sexual maturity provide information used in protecting the brood stock and rate of maturity indices are more recent examples of these management initiatives.

The trend in time responses (mean age, age to maturity, catch per unit effort, etc.) to exploitation of walleye stocks in the Great Lakes and larger inland lakes illustrate the appropriateness of monitoring these variables. Age to maturity, mean age of the catch, and fecundity will also be useful variables in determining the compensatory reserve to population reduction among walleye stocks inhabiting various energy and nutrient regimes. Using examples of heavily exploited walleye populations, we have made an initial attempt to show the degree of compensation in different energy regimes. A crisis curve is given to warn when various walleye stocks are in danger of collapse due to commercial overexploitation.

Key words: walleye, phenotypic and genotypic difference, stock, distribution, rate of maturity, fecundity, walleye management

COLBY, P. J., AND S. J. NEPSZY. 1981. Variation among stocks of walleye (*Stizostedion vitreum vitreum*): management implications. Can. J. Fish. Aquat. Sci. 38: 1814–1831.

L'identification de races, lignées ou sous-populations de dorés jaunes par examen de différences morphologiques ou biochimiques a connu un succès relativement limité. Bien

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qu'on ait des indications que des différences entre stocks peuvent être génotypiques, la plupart des données indiquent que ces différences (âge, croissance, féconditié, maturité) sont des expressions phénotypiques de l'influence du milieu. En l'absence de preuves génétiques, les différences biologiques fournissent donc un moyen fiable d'identifier et de gérer les stocks de dorés jaunes.

Les populations de cette espèce sont distinctes dans l'espace, montrant dans leur aire de distribution de grandes différences de taux de croissance, taux de maturité et longévité. Il est probable que toute expression génotypique de ces caractéristiques de populations seraient masquées par des influences de l'environnement. Il n'existe pas de preuves concrètes que les différences de croissance, âge de maturité, fécondité et longévité parmi les dorés jaunes sont héréditaires. Le fait que les populations méridionales doivent se reproduire en rivière laisse à penser qu'il s'agit de différences génétiques, mais ceci reste à prouver.

Certaines des variables physiologiques utilisées pour délimiter les réponses des stocks à leur environnement peuvent être des outils de gestion utiles quand il s'agit de mesurer la façon dont ils réagissent à diverses perturbations, telles que l'exploitation et la modification de l'habitat. L'aptitude relative des espèces à se renouveler est une mesure de la fécondité spécifique. La détermination de l'âge moyen de capture et l'âge du début de la maturité sexuelle sont des données qu'on utilise pour protéger le stock reproducteur, et les indices du taux de maturité sont des exemples récents de ces initiatives de gestion.

La tendance observée dans les réponses temporelles (âge moyen, âge de maturité, PUE, etc.) à l'exploitation du doré jaune dans les Grands Lacs et dans les autres grands lacs de l'intérieur montre bien l'importance de surveiller ces variables. Parmi les stocks de dorés jaunes habitant dans divers régimes d'énergie et de nutrition, l'âge de maturité, l'âge moyen de capture et la fécondité seront également d'utiles variables dans la détermination de la réserve compensatoire de l'espèce à une diminution d'effectif de population. Nous avons tenté, à l'aide d'exemples de populations de dorés jaunes lourdement exploitées, de démontrer le degré de compensation à divers régimes énergétiques. Nous présentons une courbe de crise qui signalera le danger quand des stocks de dorés jaunes sont exposés à un affaissement à la suite d'une surexploitation commerciale.

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MOST measurable differences between fish stocks are either phenotypic, genotypic, or experimental error. Most describable differences among walleye (*Stizostedion vitreum vitreum*) stocks are presumed to be phenotypic in response to environmental stimuli, or at least have not been proven to be genetic or inheritable differences. Compared with salmonids, walleyes are widely distributed, originally living in climatic zones reaching from the Gulf Coast in Alabama and the Pearl River in Mississippi to the McKenzie River in the Northwest Territories. Walleyes are far ranging, migrating several hundred kilometres during spawning, and although homing to specific spawning grounds they are not as obligative as salmonids. Usually some spawn on grounds other than those considered home grounds. It is presumed that there is a greater flow of genetic material among these species than among salmonids, especially in large open systems. Also, walleyes have been introduced in areas within and outside their natural range to the extent that there has been intermixing of stocks.

The purpose of this paper is to review reported biological differences among walleye stocks and to show how these differences can be useful in managing this important resource and how future studies to identify differences may be beneficial to management. Also, suspected inheritable differences between stocks of walleye may be masked by phenotypic differences imposed by different energy regimes throughout their distributional range.

Evidence of Stock Differences

BIOCHEMICAL DISCRETENESS

Identification of races, strains, or subpopulations of walleyes by examining differences in their biochemistry has met with relatively limited success. No practical procedure has yet been standardized for the purpose of identifying discrete walleye stocks for management purposes.

Starch gel electropherograms of muscle myogens showed a polymorphism involving three patterns (Uthe et al. 1966). The distribution of these patterns was consistent with the two glacial refugia postulated for this species (Radforth 1944), with a possible intermixing of the two subpopulations in the Great Lakes and tributary waters (Uthe and Ryder 1970). The plasma proteins were variable but within the limits of species specificity.

Vely (1970) sampled walleyes from 15 locations over the following geographical areas: Ohio, Michigan, Ontario, Pennsylvania, New York, Minnesota, and Manitoba. A comparison of band patterns between these groups indicated many points of similarity with only a few less prominent points of difference that were not considered sufficient to indicate a basic dissimilarity in plasma protein composition between walleyes from various ecosystems.

Ulrikson and Laarman (1971) collected walleye during

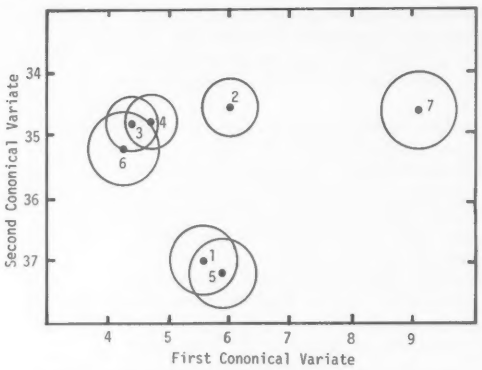

FIG. 1. The first two canonical variates from the mean vectors of walleye for seven collection sites. Circles denote 95% confidence limits. (From Ulrikson and Laarman 1971.) 1, Muskegon River; 2, Sandusky Bay; 3, Pointe Mouillee; 4, Port Clinton; 5, Huron River; 6, Thames River; 7, Manistique Lake.

1969 spawning runs from three sites on Lake Erie, a tributary of Lake St. Clair (Thames River), and in Michigan from Manistique Lake (Mackinac County), Muskegon River (Newaygo County), and Huron River (Washtenaw County). Six major serum protein bands were evident on the electrophoretic gels from all the walleyes. Their analysis showed four groupings: (1) Muskegon and Huron rivers; (2) Sandusky Bay; (3) Pointe Mouillee, Port Clinton, and Thames River; and (4) Manistique Lake. The authors suggested that the Sandusky Bay walleyes may be a genetically discrete subpopulation, as they were the only group which could be separated from the other three collections taken from Lake Erie and the Thames River (Fig. 1). Their objective of separating four genetically different subpopulations among walleyes sampled in the Lake St. Clair and Lake Erie area by electrophoretic patterns of serum proteins was not accomplished. Thus, they concluded that either genetic differences do not exist between these groups, or other tissue proteins or enzymes may be more useful for this purpose.

Electrophoresis of extracts of white skeletal muscle of walleye revealed a total of six phenotypes of malate dehydrogenase *MDH* isozymes. The heritabilities of the six phenotypes were tested in a breeding experiment and provided evidence for the existence of three nondominant alleles at one *MDH* locus. The allele frequency varies in walleyes from four Canadian locations (Clayton et al. 1971). Identification of supernatant and mitochondrial isozymes of *MDH* on electropherograms was also used to separate *S. vitreum* from *S. canadense* and their suspected interspecific hybrids (Clayton et al. 1973).

In a subsequent study, Clayton et al. (1974) described the distribution of supernatant *MDH* phenotypes in several walleye populations in western Canada. They calculated gene frequencies and the Castle–Hardy–Weinberg distribution of phenotypes, and found the frequency of one allele to decline in populations only a relatively short distance downstream from headwater lakes. Although they suggested hypotheses to explain their findings, they realized present knowledge regarding the real nature of *MDH* alleles was limiting. They believed, however, that alleles have practical value as a biological "tag." Subsequently, this isozyme tagging procedure (Clayton et al. 1971, 1974) was used as a means to separate native from introduced stocks, thus permitting successful evaluation of walleye fry introductions into West Blue Lake, Manitoba (Ward and Clayton 1975; Schweigert et al. 1977).

MORPHOLOGICAL DISCRETENESS

Definitions of subpopulations of walleyes on the basis of morphology alone have been unsuccessful. Recently, a new method of quantifying fish scale shape, and demonstrating its use in a problem of fish stock identification, has been introduced by Jarvis et al. (1978). They quantified the planar shape of walleye scales by a method of unrolling the digitized scale outlines and describing the resultant series by Fourier series analysis. For a thorough description of technique see Casselman et al. (1981).

The method was used in an attempt to discriminate stock scale samples of 5-yr-old male walleyes from two spawning locations in eastern Lake Erie (one a riverine population at Cattaraugus Creek, the other a shoal population at Seneca Shoal).

Walleye stocks in western Lake Erie are composed of a number of presumably discrete spawning stocks, which may mill or continue to be discrete during the year. Scales from spawning walleye populations in western Lake Erie were analyzed with this method, and results showed fish from the Maumee River, Sandusky River, and Toussaint Reef, Ohio, could not be assigned to their stocks of origin based on their scale shapes (Riley 1981).

PHYSIOLOGICAL VARIATION

In regard to the STOCS concept, changes in inheritable growth patterns due to gear selectivity as described by Handford et al. (1977) for whitefish (*Coregonus clupeaformis*) were not apparent to investigators analyzing long-term walleye harvests.

However, differences in walleye growth due to climate are quite apparent, and any departure in growth due to genetic differences will have to account for these environmental effects.

The greatest reported growth rate of walleyes occurred in Texas reservoirs among walleye stocks originating from Iowa (N. Carter, personal communication) planted in Lake Meredith, Texas, and subsequently introduced from the latter lake into other reservoirs (Prentice and Clark 1978). Length at first annulus varied from 76 mm for walleyes (sexes combined) from Makoop Lake and for male walleyes from Lake Attawapiskat (both in northern Ontario) to 467 mm for females from Belton Reservoir in Texas (Colby et al. 1979). The smallest length at first annulus (67 mm) was from Killens Reservoir, Montana, but there is some doubt about the annulus (J. C. Peters, personal communication).

Mean growing degree-days above 5°C (GDD > 5°C) were calculated from meteorological data nearest the study areas to determine a possible relationship between energy absorbed in the water column and age to maturity and longevity of walleyes. A workable modification of Treidl's formula (Treidl

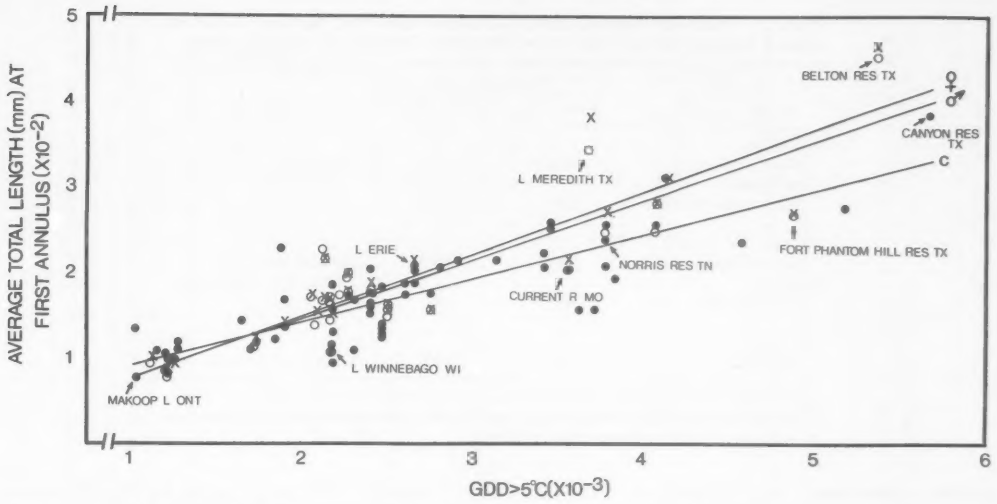

FIG. 2. Mean total lengths at first annulus versus growing degree-days above 5°C for Walleye from various water areas in North America (× = ♀, 0 = ♂, ● = combined sexes, including unidentified immature fish). The respective correlations (all significant, $P < 0.05$) for females, males, and sexes combined are as follows: $Y = 2.890 + 0.073X$, $r^2 = 0.812$, $n = 33$; $Y = 6.673 + 0.069X$, $r^2 = 0.802$, $n = 34$; and $Y = 38.201 + 0.051X$, $r^2 = 0.723$, $n = 67$ and is a separate set of data, not ♀ + ♂ above.

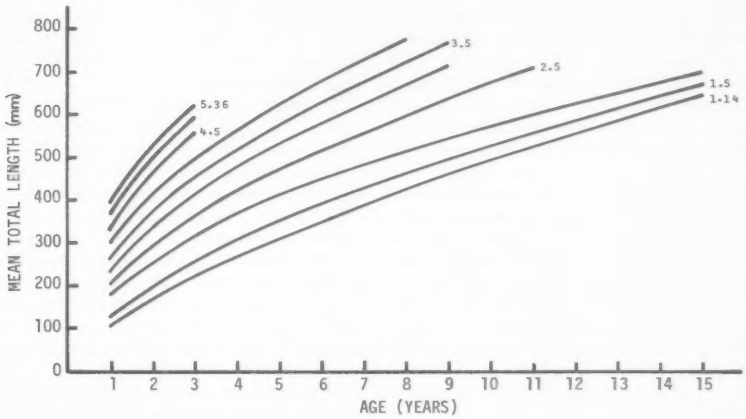

FIG. 3. Relationship between mean total length (mm) at annulus and age of female walleyes over a major portion of their distributional range. The curves were derived from points plotted from curvilinear relationships between mean total length at annulus of females from various walleye populations and GDD > 5°C for ages 1 through 15. The curves describe the length–age relationships for 1500 to 5000 GDD > 5°C and the ranges (1140 and 5360), expressed as GDD > 5°C ($\times 10^{-1}$), representing the limits of the data.

1976) for converting U.S. weather data to GDD > 5°C from GDD > 40°F and GDD > 43°F is:

$$\text{GDD} > 5°\text{C} = 5/9[G_{40} - 1/3(G_{40} - G_{43})]$$

where G_{40} and G_{43} are growing degree-days above 40 and 43°F. Canadian data were taken from Aston (1977a, b, 1978a, b). Calculating GDD > 5°C for certain remote water bodies required averaging adjacent stations.

There were significant correlations ($P < 0.05$, ANOVA) between accumulated GDD > 5°C and length at first annulus for walleyes, sexes separate, and combined (Fig. 2, 3). These data points, from a corrected Appendix 1 of Colby et al. (1979), represent 87 observations at 78 stations or water bodies. They consisted of 73 back-calculated lengths, 10 total lengths determined at the end of each growing season

TABLE 1. Relationship between cooling degree-days below 10°C (necessary to cool the water in Southern reservoirs) and walleye reproduction. DD_C data are 1941–70 normals.

Reservoir (station location)	Degree-days (DD_C) Above 5°C	Below 10°C	Comments
El Capitan (San Diego)	4436	23	No natural reproduction
Casa Blanca[a] (Brownsville-Del Rio)	6284	79	
Medina (San Antonio)	5680	134	Some reproduction following cold winters
Canyon (San Antonio)	5680	134	
Meredith (Amarillo)	3692	860	Good natural reproduction

[a]Data reflect average of these two stations and are an approximation of weather conditions at Casa Blanca Reservoir. Walleye are no longer caught in this reservoir and are assumed not to be present (Prentice personal communication).

(summer measurements were excluded) and four studies containing a combination of observed lengths at the end of the growing season with back-calculated lengths for the early ages (primarily I and II which were absent from the samples). We feel that these data are adequate for describing relationships between walleye growth and energy availability expressed as GDD > 5°C. Notice in the south, where the growth rate is fast, the female walleye life span is shorter and in the north, where their life span is much longer, their growth is slower (Fig. 3). The optimum energy regime for good average size (a combination of longevity and growth rate) seems to be from about 2500 to 4000 GDD > 5°C.

The final years of several now defunct marine fisheries appear to have been marked by substantial changes in growth parameters in the waning years of target species (G. Hirschhorn, personal communication). Change in growth of walleyes in Lake Erie during the fishing up process was described by Schneider and Leach (1977). Similarly, Parsons (1967) reported that blue pike (*Stizostedion vitreum glaucum*) which had completed four growing seasons were approximately eight times heavier in 1959 (1.3 kg), following heavy exploitation, than in 1951 (0.17 kg) and considerably longer (48.0 cm as compared with 28.4 cm). Introgressive hybridization (Regier et al. 1969) between walleyes and blue pike may have been occurring and genetic differences in growth were also being expressed.

Maturation and age to maturity — Age to maturity varies considerably between walleye stocks and generally correlates inversely with growth rate which in turn is greatly influenced by energy availability. In aquatic environments receiving too much energy, instead of early maturation, maturation may not occur at all even though growth is excellent. Thus, water temperatures which are too high during the time of maturation may limit the southern distribution of walleyes.

A minimum winter temperature of 10°C is near the upper limit for maturation of gonads in yellow perch and walleye (Hokanson 1977). Walleyes failed to reproduce in southern California reservoirs which became essentially isothermal in winter with temperatures ranging from 10 to 12.5°C (Miller 1967; Hokanson 1977). In El Capitan Reservoir, California, there is no reproduction of walleye (Miller 1967), nor is there any in Casa Blanca Reservoir, Texas, near the Mexican border (J. Prentice, personal communication). However, in Canyon and Medina reservoirs there is limited reproduction during cooler winters (J. Prentice, personal communication) and good reproduction in Lake Meredith. Thus, Texas winters are sufficiently cool to permit reproduction of walleyes in some of their reservoirs even though the summers may experience more degree-days above 5°C than at San Diego, California (Table 1).

The environment greatly influences the rate of maturity of walleye (Table 2). Northern stocks mature later and over a greater number of years than southern stocks and heavily exploited stocks (Wolfert 1969; Spangler et al. 1977). Bond et al. (1978) reported that male walleyes do not spawn before reaching age 7 and females before age 8 in the Hay River, Northwest Territories. The GDD > 5°C in this part of Canada is 1000. Rawson (1957) reported that a few walleyes in Lac La Ronge spawned at age 5 but the bulk of the run was 8–10 yr of age. In Savanne Lake, Ontario (GDD > 5°C = 1287) female walleyes first mature at 5 (43%) and are not completely mature until age 9 (D. Romani, unpublished data). Most male walleyes in the Moon River stock mature by age 4 and females are mature at age 5 (Winterton 1975), which is similar to other Lake Huron stocks (Payne 1965). In Lake Erie where walleyes mature at ages 2 and 3 (Wolfert 1969) heavy exploitation on the stocks caused an increase in growth rate (Regier et al. 1969). Subsequently, the growth rate of walleyes appears to be fluctuating and maturity is occurring a little later as the stocks build up following closure of the fishery because of mercury contamination. D. R. Wolfert (personal communication) has found no recent trend in diminishing growth rate and suggests that there appears to be a shortage of forage, with the energy ingested going to growth and subsequently less available for maturation. This is quite likely for earlier maturing females characteristic of the walleye population in western Lake Erie. Nikolsky (1965) has reported this observation for other fish species. He generalizes that a larger proportion of the food intake goes to the formation of fat

TABLE 2. Relationship between rate of maturity of female walleyes and growing degree-days above 5°C (GDD > 5°C). Given also are the relative fishing pressure (RFP) on the walleye stock as surmised from personal communication and the literature: L = lightly fished, M = moderately fished, H = heavily fished, N = negligible fishing, and ? = unknown. Type of fishery: C = commercial fishery, A = angling, and E = experimental fishing using various gear. Time of year the stocks were sampled for estimating maturity: Sp = spring, Su = summer, F = fall, W = winter, and U = unknown. Percentages in parentheses not calculated by original authors, but from the data given in their papers (for Pike Lake only assumed 1:1 sex ratio among two immature fish used in calculations); those percentages in brackets are females which were developing at time of sampling (TOS) but had not yet attained maturity.

Location	Age at maturity (females)[a]									GDD > 5°C	RFP	TOS
	2	3	4	5	6	7	8	9	10			
Mosquito Cr., NWT[f]							×[b]	(65.4)	(100.0)	967	L-M;A	Sp-Su
Southern Indian L., Man.[g]				×[c]				××	××	1013	M;C	Sp
Hay R., NWT[h]							×[d]		×	1022	M;A	Su
Big Trout L., Ont.[i]					50.0	100.0				1043	?;C	U
N. Caribou L., Ont.[i]						71.0	80.0	88.0	100.0	1156	?;C	U
Lac La Ronge, Sask.[j]				×[e]		50.0	××	××	××	1178	?;C,A	Sp
Deer L., Ont.[i]					33.0	43.0	93.0	100.0		1281	?;C	U
Savanne L., Ont.[k]				43.0	75.0	86.0	78.0	100.0		1287	N;E	F
Dexter L., Ont.[l]			(25.0)	(37.5)						1287	L;A,E	Su
L. Winnipeg N., Man.[m]			5.3	10.4	28.1	50.0	58.3	100.0		1422	M;C	Su,F
L. Winnipeg S. Man.		2.3	8.3	3.0	14.3	0.0	0.0	0.0		1631	H;C,A	Su,F
		[0.0]	[2.4]	[9.1]	[25.0]	[60.0]	[50.0]	[100.0]				
L. of the Woods, Ont., MN[n]			4.0	33.8	31.2					1657	H;C,A	W,F
Escanaba L., WI[o]			43.0	83.3	75.8	85.2	100.0			1901	H;A	F
Georgian Bay, Ont.[p]			×	××						1906	H;C,A	Sp
L. Winnebago, WI[q]			8.0	32.0	67.0	81.0	100.0			2187	M;A	F,W
Pike Lake, WI[r]		×	(99.0)	(100.0)						2273	H;A	Sp
Western L. Erie[s]	1.0	100.0	98.6							2600	H;C,A	W,F,Sp
		86.3−										
L. Meredith, TX[t]	(36.0)	××								3691	L;A	Sp
Center Hill Res., TN[u]	(26.3)	(80.0)	(100.0)							4078	L;A	Sp
Canton Res., OK[v]	6.2	88.9								4145	L;A	Sp
El Capitan Res., CA[w]		××								4436	L;A	W,Sp
Canyon TX[x]	×	××								5680	L;A	W,Sp

[a]Percentages of mature fish from the total number of fish sexed in a certain age-group; where we were unable to calculate percentages, × refers to age at first maturity and ×× refers to age(s) where most mature or modal age(s) where most fish appear to be reaching maturity.

[b]The few (6) females were 100% mature, but not considered representative of the actual percentage reaching maturity of that age-group since so few were captured.

[c]Youngest mature females were age 5, but modal ages were ages 9 and 10.

[d]Females do not spawn before age 8, youngest spent female observed by Bond et al. (1978) was age 10.

[e]A few age 5 females enter spawning run, but bulk of the run was ages 8−10.

[f]Falk et al. (1980), Gillman (personal communication. [g]Bodaly (1980). [h]Bond et al. (1978). [i]Armstrong (1961). [j]Rawson (1957). [k]Romani (unpublished data). [l]Moening (1975). [m]Lysack (1980). [n]Carlander (1945). [o]Serns (unpublished data). [p]Winterton (1975). [q]Priegel (1969). [r]Mraz (1968). [s]Parsons (1972). Wolfert (1969). [t]Kraai and Prentice (1974). [u]Muench (1966). [v]Grinstead (1971). [w]Miller (1967). [x]Prentice (1977, personal communication).

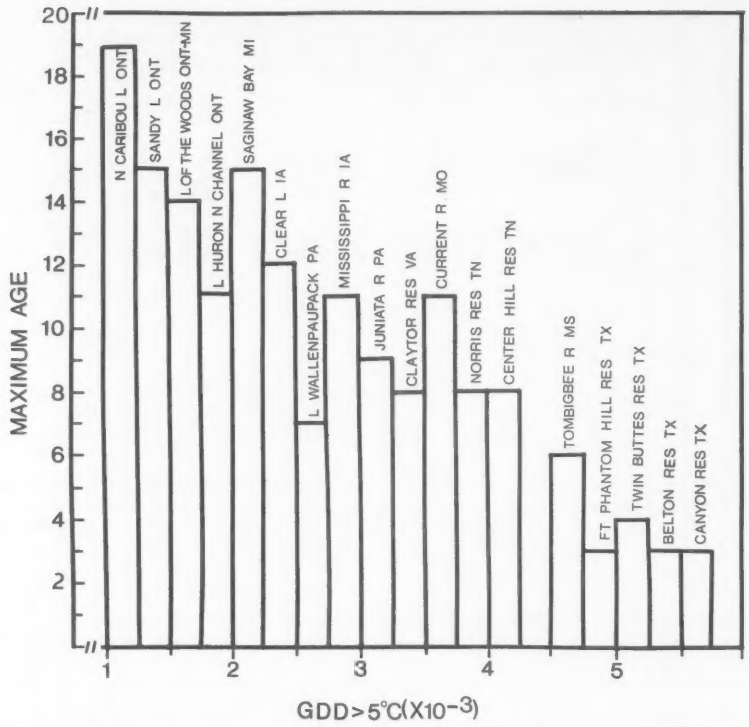

FIG. 4. Relationship between maximum scale age of walleye from various areas of North America from published literature and growing degree-days above 5°C (in increments of 250).

reserves in older fish, while a larger proportion goes to protein growth in fish that spawn first. Thus, starvation of the older fish has less impact on fecundity and egg quality. In Canton Reservoir, Oklahoma, where 1st-yr growth is exceptionally great, nine age 1 males were found to be sexually mature along with 6.2% of the age 2 females (Grinstead 1971). In Medina and Canyon reservoirs, Texas, male walleye mature at age 2 with some females maturing at age 2 but mostly at age 3. A trend toward an earlier age of maturity among the more rapidly growing fish, both males and females, is apparent from the literature (Colby et al. 1979).

Age at maturity of walleyes is responsive to exploitation. Changes in the rate of maturity for managing the species in Lake Winnipeg have been analyzed (Lysack 1980). The analysis consists of fitting a logistic type curve to a plot of frequency of mature fish versus age and it may be an improvement over that developed by Abrosov (1969).

Longevity — The average life expectancy of walleyes (Fig. 4) varies from about 12–15 yr near the northern limits of their range to about 5–7 yr at the extreme southern limits (Colby et al. 1979; Olver 1964). In general, where walleyes grow fast they mature early and their life span is shorter. The maximum reported age for a walleye is 20 yr (Scott and Crossman 1973). However, on the basis of estimated ages from tagging and known periods of liberty, three male walleyes, jaw-tagged in 1947 in Lake Gogebic, Michigan, and recaptured 16, 17, and 18 yr later were estimated to be 26, 23, and 23 yr old, respectively (Schneider et al. 1977). Walleyes older than 20 yr may be more common than previously expected. Walleyes 23–28 yr old were aged in Manitoba using otoliths (W. Lysack, personal, communication).

Although planted walleyes have been in Casa Blanca Reservoir, Texas, for 9 yr, the maximum age is 5 yr. These fish reach weights of 1.4–1.6 kg in their 1st yr of growth. In Lake Meredith, Texas, where no heavy exploitation occurs, the oldest walleye is 9 yr old (J. Prentice, personal communication).

In Ontario, anglers generally catch younger fish than commercial fishermen (Elsey and Thomson 1977; Winterton 1975), and subsampling the catches of either fishery would not give a true age structure of the population. Older fish, necessary for determining longevity, are less likely to show up in the catch of anglers due to differential selectivity of younger fish by anglers (Serns and Kempinger 1981).

Walleyes seem to follow Rubner's hypothesis for poikilotherms that longevity is inversely proportional to intensity of living (Allee et al. 1949). This relationship is also strongly apparent for the European pikeperch, *Stizostedion lucioperca* (Popova and Sytina 1977). Undoubtedly, there are older fish

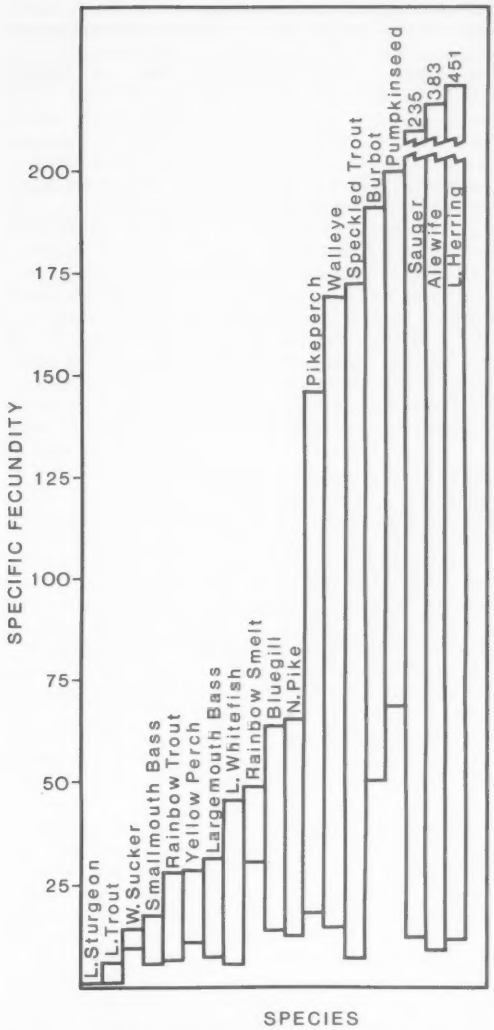

FIG. 5. Specific fecundity (Iogansen's method) of various fish species from the Great Lakes and other inland lakes, and of the European pikeperch (*Stizostedion lucioperca*). Iogansen's (1955) formula is: specific fecundity = $pj\sqrt{rx}$ where r = the number of eggs produced per fish per year, x = the total number of spawnings per fish per lifetime, j = the age of sexual maturation, and p = the interval between spawning years per fish.

than reported in the literature, but we feel that the general trend of decreasing longevity with increasing growing degree days is valid (Fig. 4).

Fecundity — Fecundity of walleyes is quite variable and probably reflects differences in population density and subsequent abundance of food, as evidenced for other species of fishes from the Soviet literature (Nikolsky 1965) and differences in community structure. These relationships are not available for North American walleye populations.

Walleyes are prolific spawners, with considerable variation in fecundities. A review of walleye fecundity is given in Colby et al. (1979).

Various specific fecundity indices were calculated by manipulating high and low fecundities reported in the literature for various species and their early and late age to maturity, and also their range in longevity. Thus, using various combinations of the variables which seemed likely to occur in nature, the specific fecundities were calculated with their suspected range (Fig. 5).

The relationship is extremely general and lacks the inclusion of all the variables which can affect population fecundity, e.g. the relative abundance of the various year-classes, each with their own range of fecundity, environmental influences, and hatching success. Different geographical areas and aquatic systems from which various data were gathered created great variation in the index. Thus, the index may be overresponsive and exaggerate reproductive potentials.

Figure 5 supports Adams' (1980) comments that a species is not going to be an *r* or *K* strategist in an absolute sense, but will occupy a relative position on the *r* and *K* continuum (especially those species listed on the far right-hand side of Fig. 5). For example, specific fecundity for older maturing walleyes from Lake of the Woods was 15 (data from Carlander 1945) and 144 for the faster growing and earlier maturing walleyes in the western basin of Lake Erie (data from Wolfert 1969). Both values are within the range hypothesized in Fig. 5.

We believe this index, as well as being an approximation of a species' reproductive capacity or potential intrinsic rate of increase, also reflects to some degree the potential ability of a species to elevate its fecundity in response to environmental or exploitive pressures. The ranges in the index for various species show a great variability within species, especially of those fishes whose specific fecundity increases rapidly in higher energy regimes (right side of Fig. 5). Lake sturgeon and salmonids (especially lake trout) have low indices and lack the relative potential to elevate production in response to environmental changes or to increased exploitation. Conversely, lake herring (*Coregonus artedii*), alewife (*Alosa pseudoharengus*), walleye, and centrarchids have an elevated potential to respond to such changes. Thus this simple model provides an insight into how fish communities in different energy regimes may change in structure when perturbed.

Parasites — Colby et al. (1979) listed known parasites of adult walleyes, with additional information on intensity of individual and population infections. We examined some current data on parasites in walleyes from various lakes (A. O. Dechtiar and S. J. Nepszy, unpublished data; A. O. Dechtiar, personal communication) to determine if there was any evidence for stock discreteness according to parasite diversity and loading.

Although there were differences in parasitic loading between different populations reflecting the nature of the environment (Table 3), there were no useful parasitic tags to identify discrete stocks.

TABLE 3. Checklist of parasites of walleyes from the Ontario waters of various lakes.

Taxonomic group	Lake of the Woods	Superior	Huron	St. Clair	Erie	Ontario
Protozoa						
Myxobolus						×
Monogenea						
Cleidodiscus aculeatus	×	×	×	×	×	×
Cleidodiscus sp.				×		
Digenea						
Tetracotyle					×	×
Diplostomum spathaceum				×	×	
Centrovarium lobotes				×	×	
Sanguinicola occidentalis		×	×	×	×	×
Azygia angusticauda	×			×	×	×
Bucephalus					×	
Crassiphiala bulboglossa			×	×	×	
Bunodera sacculata	×			×		
Clinostomum marginatum	×					
Diplostomulum scheuringi	×					
Diplostomulum sp.	×					
Tetracotyle communis	×			×		
Phyllodistomum superbum	×					
Diplostomulum flexicaudum			×			×
Bucephalus pusilla				×		×
Uvulifer ambloplitis						×
Tetracotyle diminuta		×				
Cestoda						
Bothriocephalus cuspidatus	×	×		×	×	×
Proteocephalus stizostethi	×		×	×	×	
Triaenophorus stizostedonis	×			×	×	×
Proteocephalus ambloplitis	×			×		
Nematoda						
Spinitectus gracilis					×	
Camallanus oxycephalus					×	
Contracaecum brachyurum	×		×	×		
Eustrongylides sp.	×					
Dacnitoides cotylophora						×
Eustrongylides tubifex						×
Raphidascaris acus				×		
Acanthocephala						
Neoechinorhynchus tenellus	×	×		×	×	×
Neoechinorhynchus cylindratus				×	×	
Leptorhynchoides thecatus					×	×
Metechinorhynchus salmonis	×	×				×
Neoechinorhynchus rutili						×
Crustacea						
Ergasilus luciopercarum		×	×	×	×	×
Ergasilus caerulus	×			×	×	×
Argulus canadensis	×					
Argulus versicolor	×					
Ergasilus centrarchidarum	×					
Mollusca						
Glochidia	×			×	×	×
Other						
Myzobdella moorei						
Saprolegnia						
Lymphocystis (virus)	×	×	×		×	×
Illinobdella moorei	×			×		
Sample size	29	15	26	96	75	37
Species of parasites	23	8	8	22	20	20

Behavioral movements — Although there is some understanding of the distances walleyes travel, both as individuals and in groups, we need more clarification for a better understanding of the discreteness of subpopulations. We need to know (a) the degree to which walleyes intermingle or separate in space and time, (b) the extent of seasonal separation of various age-groups, (c) the degree, if any, that walleyes are obligative shoal or riverine spawners, and (d) the extent to

which homing among walleyes is the result of imprinting or learned behavior.

Under present quota management practices it is customary to divide large bodies of water into separate basins or subbasins and determine a quota for each, taking into consideration past species history, productivity of the basins, and protection of discrete stocks. For example, Lac Seul, a lake in northwestern Ontario with an area of 129 500 ha, has 23 basins and each basin contains walleyes having, as expected, their own size and age structure, and, to some extent, seasonal vulnerability to angling. To manage these separate basins as having their own discrete stocks would cause serious management errors. Certain basins with a low mean age relative to the age at maturity would be considered overfished, while basins with an older age structure would be considered underfished. If walleyes separate by age-groups, we may be encouraging overexploitation of brood stocks in basins with a higher mean age, and underutilization of fish in basins with a lower mean age. Therefore, it is advantageous to understand behavior and be able to distinguish between stocks, especially in large bodies of water.

There is some evidence that younger fish, many immature, do not travel as great a distance as the older members of the stock (Wolfert 1963; Priegel 1970; Winterton 1975). Wolfert (1963) found in Lake Erie that more walleyes tended to travel greater distances as their ages increased, and Priegel (1970) found in both the Fox and Wolf rivers in Wisconsin that younger age-groups of walleyes did not migrate as far upstream as did older age-groups.

At least two discrete populations of walleyes are evident in Lake Erie, one largely confined to the western basin and a smaller population to the eastern basin (Wolfert 1963; Wolfert and Van Meter 1978). If the definition of stocks as groups of fish associated with a particular spawning area (reproductive isolation) is accepted, then there is some limited current evidence for a number of discrete stocks of walleyes within the western basin.

Ferguson and Derksen (1971) found that among walleyes tagged in the mid-1950s prior to October in the central basin of Lake Erie, subsequent recoveries made in the spring encompassing the spawning period suggested a variety of general spawning locations utilized by these fish. Most, in fact, were recovered in or near the western basin.

Payne (1963) reported in the late 1950s and early 1960s that a migration of walleyes from the Upper and Lower Bay of Quinte of Lake Ontario took place after spawning. Involved in this migration were approximately 47% of age 4 fish, 70% of age 5 fish, and more than 80% of the fish in the older age-groups. In May, the migration was less than half complete at age 4 but more than 75% complete at older ages. These fish returned to the Bay during the late summer and early fall.

Postspawning movements of walleyes are not random, but directed toward the cooler, deeper water of Lake Ontario; Upper Bay fish pass through the Lower Bay enroute to and from Lake Ontario.

Further evidence of the separation of age-groups, with the older fish being the first to move to the cooler and deeper waters of the Great Lakes with the advent of summer, is provided by Winterton's (1975) observations reported on the seasonal movement of Moon River walleyes into Georgian Bay. Analysis of tag returns from anglers and commercial gill-netters provides evidence that walleyes moved out through the islands area from May to July, during which time they were vulnerable to angler harvest. Experimental trapnetting in the Moon River Islands area during the summers of 1968–71 and onshore gillnetting in 1971 indicated that older members of the stock (>5 yr) had vacated the onshore area during this period. By July, walleyes were appearing in gillnet fisheries about 35 km north and south of the spawning site, but principally in the Watchers Islands area. Walleyes remained on the summer grounds until October and November, when they moved back towards the Moon River, again providing an onshore angling fishery.

Homing — Some observations suggest that adult walleyes in certain populations migrate between home spawning and home feeding areas (Crowe 1962; Olson and Scidmore 1962; Forney 1963). Olson et al. (1978) feel that homing is probably an adult learned behavior influenced by physical characteristics of the environment and likely strengthened by repeated migrations. They suggest that dispersal of walleye eggs and fry from the site of egg deposition by wind and river currents precludes natal-induced behavior. They also postulated that if homing is indeed an adult learned behavior, the reestablishment of spawning runs in once-polluted but rehabilitated rivers might be improved by transplanting adult walleyes from other waters during spawning migration.

The discreteness of spawning grounds seems to depend on their remoteness from each other. Whitney (1958) found that walleyes spawning in two locations that were only 2.8 km apart in Clear Lake, Iowa, intermingled extensively, and this appeared to be the case with the Moon River and Blackstone River (which is within 10.5 km of Moon River) walleye, as shown by the fact that walleyes tagged in Moon River from 1968 to 1970 were present at Blackstone River in 1971 (Winterton 1975). However, Eschmeyer (1950) concluded that walleyes remained restricted to a small area during spawning season, and Forney (1963) found that spawning runs 11.3 km apart in Oneida Lake did not intermingle.

Van Vooren (1978) suggested that the walleye population in western Lake Erie is not homogeneous. Spawning populations were discrete to each of two major spawning tributaries and a major spawning reef (Sandusky River, Maumee River, and Crib Reef). He suggested that these populations were discrete to a particular reef within a reef complex, although subsequent postspawning tag returns indicated that some of these fish moved progressively northward and mixed in the Detroit River outfall area. He also found significant differences in the relative year-class strength and age composition between the three spawning populations. Recaptures of tagged walleyes which returned to spawn 1 and 2 yr after tagging showed each of the populations studied to be discrete. Postspawning tag recoveries during June–September with significantly different mean ages indicated that the three subpopulations possibly remained partially discrete during the summer feeding period (Van Vooren 1978).

Further evidence of the discreteness of walleye populations is provided in the Bay of Quinte. Many of the walleyes which spawned in the Upper Bay of Quinte remained there during the summer months, becoming localized at the mouth of the Trent River. More than 2.5 times as many of the fish tagged

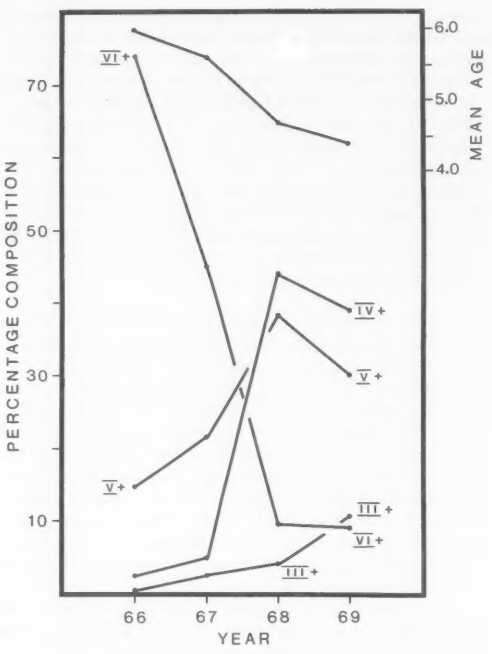

FIG. 6. Weighted mean age and age composition (%) of catch of walleye from the commercial fishery in Black Bay, Lake Superior, 1966–69 (C. A. Elsey O.M.N.R., Thunder Bay, Ont., unpublished data).

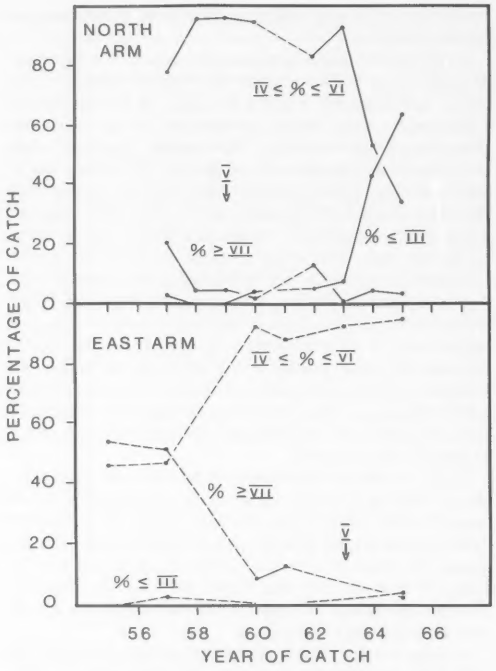

FIG. 7. Percentage of catch of various aged walleye from commercial catches in Rainy Lake, 1955–65 (J. Chevalier, O.M.N.R., Sudbury, Ont., unpublished data). Arrows indicate years mean age of the catch dropped to 5.

in the vicinity of Belleville and Trenton were recovered in the Trent River at Trenton or elsewhere in the Upper Bay. Since none of the fish tagged in Hay Bay were recovered west of Belleville, it may be assumed that the "group" of Upper Bay fish situated at the mouth of the Trent River was distinct from the Lower Bay "group" throughout the year.

Hackney and Holbrook (1978) observed that southern walleye stocks were unable to sustain themselves in reservoirs, but that fisheries recover when the reservoirs are restocked with northern strains (Cayuga Lake or Lake Erie) which spawn both in rivers and the lake proper. Their hypothesis that southern strains are obligative river spawners is interesting in light of the hypothesis proposed by Kitchell et al. (1977) that walleyes evolved in a riverine refugium and that their optimum habitat in lakes is similar to large temperate rivers. Thus, walleyes may have only recently (since the Pleistocene epoch) adjusted to spawning in lentic systems, as a consequence of being trapped in closed systems following the recession of glacial meltwaters.

When the St. Lawrence River was impounded for the Seaway in the late 1950s, there was a good walleye population in the river preimpoundment. When the dam was closed and the reservoir filled, walleyes moved upstream and were caught in larger numbers below the main upstream control dam. Anglers fished from shore and caught their limit within an hour or so. Then the population, possibly a riverine or lotic populations started to build up in the tributary streams on the American side of the river. Walleyes are caught occasionally now, but the population (lentic type of stock?) has never reached the preimpoundment level (J. Casselman, personal communication).

If re-introductions are attempted, care should be taken to ensure that the adult walleyes are from a system to which they cannot return. In September 1972, juvenile and adult walleyes captured at the mouth of the Current River were tagged and released at the north end of Black Bay (~150 km distance) to rehabilitate the collapsed fishery. Within 18 mo, 66 (10.6%) of the released fish were recaptured and 18.2% of these recaptures were at the Current River within 8 mo (C. Brousseau, O.M.N.R., Thunder Bay, Ont., personal communication).

Using adult walleyes from one part of a large body of water to rehabilitate another as suggested by Olson et al. (1978) may not be successful in large, open systems. Barriers of distance, direction, and possibly depth did not prevent a large portion of these transplanted fish from returning to their place of origin. It appears that stocks of walleyes in Thunder Bay and Black Bay of Lake Superior are distinct.

Using eyed-eggs, fry, or fingerlings may be an alternative. Kerner (1979) reported that re-introductions of walleye fingerlings into Sturgeon Bay, Lake Michigan, established a walleye population of 26 000 fish. The extent of natural re-

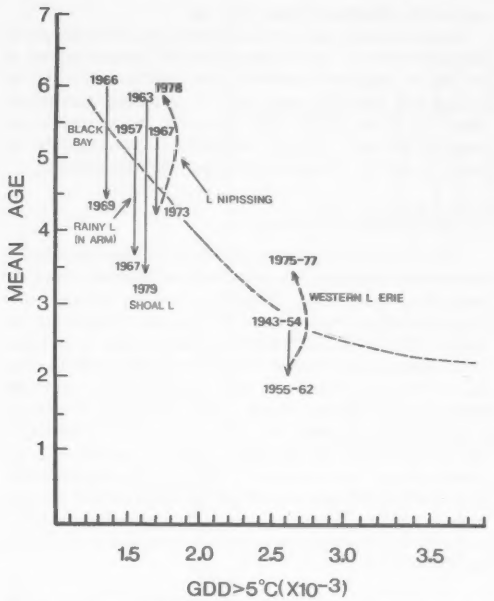

FIG. 8. Suggested relationship between the minimum scale age (weighted mean) the walleye catch can be reduced (assuming equal vulnerability of mature fish to the gear) and available energy, expressed as accumulated growing degree-days above 5°C, to permit adequate recruitment to perpetuate the stock.

production has not been determined.

Case Histories

A study of the phenotypic variation among stocks of walleyes provides excellent insights as to how these stocks should be managed. Knowledge of how growth, age to maturity, longevity, and fecundity vary between stocks inhabiting different energy regimes, and exposed to different levels and methods of harvest, provides clues to the limits that these stocks can respond to exploitation and also provides background data from which to separate environmental or genetically induced differences between stocks. Understanding phenotypic variation between ecosystems provides clues to the limits of variation to expect within an ecosystem and aids in our attempt to define discreteness of stocks.

The following brief case histories provide examples of walleye stocks responding to various levels of exploitation over a large geographical range. They illustrate the value of monitoring the phenotypic difference between stocks in various energy regimes to maximize yields.

Upper Great Lakes

Lake Superior (Black Bay) — Most of the walleyes harvested in Lake Superior were taken from Black Bay, Ontario, where annual harvests usually exceeded 50 t (Schneider and Leach 1977). The fishery completely collapsed in 1969 after a peak harvest exceeding 150 t in 1966. Overfishing was the most likely cause. Changes in age structure during the last 3 yr of the fishery, suggesting elimination of the mature stock (≥6-yr-old fish), heralded the demise of the fishery (Fig. 6). The decline of older fish from the catch and the increase in 3-yr-old fish indicated that the population was being harvested before reaching maturity and subsequently was unable to replace itself. This situation parallels the changes which occurred in the age structure of the stocks in both North Arm and East Arm of Rainy Lake (Fig. 7). Had the harvests from Black Bay been restricted to prevent the mean age of the catch from dropping respectively below 6.0 or 5.5 in 1966 and 1967, the collapse of the stock might have been prevented.

Lake Huron (Georgian Bay watershed) — Walleyes in Georgian Bay spawn in the numerous tributaries of the Bay and each stock responds uniquely to various stresses imposed on it. Excluding the Moon River stock, all have mean ages which appear too low for rebuilding the stock. Young brood stocks, such as that found in the French River with a mean age of 4.5, appear able to maintain only their present level of abundance under present pressure from both commercial and angling exploitation. Various populations in the French River system are subject to both commercial and recreational fishing.

During 1974–78 the commercial fishery was restricted and the weighted mean age of walleyes from experimental trap net catches for 1973–77 were 5.2, 5.3, 4.5, 4.5, and 5.4 respectively. The GDD > 5°C in this area of Georgian Bay is about 1750 and the mean age at which a crisis can be expected is 4.5 (Fig. 8). A mean age of 4.5 was observed in the trap nets both in 1975 and 1976, indicating that the walleyes were being pushed to the limit of their ability to compensate for exploitation. The increase in mean age in 1977 may reflect reduction of pressure on the brood stock as a result of placing a moratorium on the transfer of commercial fishing licenses and restricting commercial fishing within an area at the mouth of the main channel of the French River. However, more data are required to determine if the increase in mean age is a true trend resulting from a delayed response of reducing pressure on the walleye brood stock or just an increase in age of a stronger than usual year-class (Gunn 1979). Also, mean ages are probably very slightly underestimated because fish greater than age 10 were all assumed to be age 11 for purposes of calculation.

The Moon River stock appears to have had repeated year-class failures due to low discharges resulting from controlling water levels in upstream reservoirs (Winterton 1975) and the mean age appears to be increasing. The mean age increased from 6.6 in 1969 to 8.0 in 1972, but no age analyses have been completed since 1972.

Northern Inland Lakes

Lac des Mille Lacs — Characteristics of this lake and its fishery have been described (Elsey and Thomson 1977). The total harvest is more than double the long-term percid yields ($1.25\ kg \cdot ha^{-1} \cdot yr^{-1}$) considered maximal for commercially fished boreal lakes (Adams and Olver 1977). Greater yields in Lac des Mille Lacs probably reflect differences in harvesting methods with the predominant angling fishery having less of an impact on the brood stock than those lakes mainly supporting commercial fisheries.

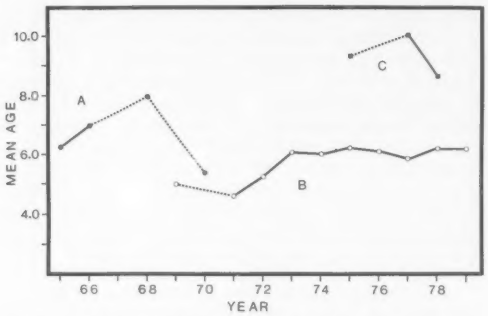

FIG. 9. Weighted mean age of walleye from Lac des Mille Lacs, Ontario, from 1965–1979. A, from commercial gillnet sampling; B, from experimental trapnetting; C, from commercial trapnetting (C. A. Elsey, unpublished data).

The small commercial fishery does not appear to be adversely influencing the older brood stock (Fig. 9). Even with the high yields the mean age of the catches using various gear has shown no downward trend characteristic of stocks prior to their collapse. The mean age of the commercial catch has not dropped below age 9.

Presently, the Lac des Mille Lacs fishery reflects the response of a walleye population or populations in equilibrium with a moderately intense angling effort (>14 h·ha^{-1}·yr^{-1}).

Rainy Lake — The annual commercial fish harvest of 4.36 kg·ha^{-1}·yr^{-1} for Rainy Lake has consistently exceeded the morphoedaphic index allowable harvest of 2.96 kg·ha^{-1}·yr^{-1}, at least until the early 1970s. The recent sport fishery harvest for walleyes may be as great as the present commercial harvest (Chevalier 1977). When the commercial catch of walleyes declined in the early 1960s, the mean age of the catch declined below age 5. At that time older fish ($\geq$7 yr) were disappearing from the catch and younger fish ($\leq$3 yr) had not begun to appear in sufficient quantity (Fig. 7).

The mean age of walleyes in large-mesh gill nets dropped to 5 yr in the North and East Arms in 1959 and 1963 (Chevalier 1977). Had the mean age been maintained above age 5, sufficient brood stock probably would have been preserved to prevent the decline of the fishery during the 1960s. Chevalier explains that to maintain a stable fishery, the average age of the Rainy Lake walleye catch should be 5.5–6.0 yr. The mean age of the catch during the mid-1960s was less than 4.5 yr in both the North and East Arms.

Lake Nipissing — The history of the walleye fishery has been reviewed to 1885 describing the factors contributing to the recent decline of the walleye fishery in that lake (Anthony and Jorgensen 1977). More recently, Jorgensen (1979) described the decline of the fishery by the decreasing catch per unit effort and changing age-class structure.

In 1967, the mean age was 5.3 yr but decreased to 4.2 yr by 1973, the year prior to restrictions. Restrictions of a reduced season for a portion of the months of March and May may have caused a recovery of older fish in the creel of anglers in subsequent years (Fig. 10).

Increase in mean age can result from lack of recruitment or increased survival. In Lake Nipissing, the increase appears to be due to increased survival, since northern pike (*Esox lucius*) also show the same trend of increasing numbers of older fish in the angler catch. However, recent surveys for young-of-the-year walleyes suggest recruitment may be increasing also (C. Jorgensen, personal communication).

LOWER GREAT LAKES

Lake Ontario (Bay of Quinte) — Trend in time data describing walleye mean age, age at maturity, or fecundity have not been determined to date. Therefore, response of these population characteristics to exploitation in Lake Ontario are unknown. However, analysis of age–length data of walleyes from spring trap net catches for 1957–62 showed that Lower Bay walleyes of both sexes were larger than those from the Upper Bay of Quinte (Payne 1963). Differences between mean lengths at age were significant ($P < 0.01$). Thus Payne concluded that the Bay of Quinte walleye population is not homogeneous, but composed of at least two subpopulations which exhibit different rates of growth and which are discrete at spawning time. Those walleyes in the Lower Bay of Quinte had an extremely rapid rate of growth compared with those in the Upper Bay.

Lake Erie–Lake St. Clair–Thames River — Examination of weighted mean ages of walleyes from various agencies and fisheries in western Lake Erie failed to provide further evidence for discrete subpopulations, but provided convincing evidence of overexploitation in western Lake Erie (Fig. 11). The mean age of walleyes taken from fall trap net catches dropped below age 2.5 at a time when 4-yr-old and older fish were disappearing from the fishery and age 1+ fish began to dominate the catch. After 1960, there was not sufficient brood stock to maintain the fishery. Although there were obvious significant differences between spring and fall catches, there were no apparent differences between areas for the years shown (Table 4). Van Vooren and Davies (1973) suggested that mixing of walleye stocks in western Lake Erie was not random during the late summer and early fall because of significant differences in mean length at age among walleyes sampled simultaneously from different areas of the basin.

Movement of walleyes between lower Lake Huron, Lake St. Clair, and Lake Erie has been documented for the mid-1950s (Ferguson and Cummins 1956; Wolfert 1963; Ferguson and Derksen 1971). Although there was some mixing of eastern, central, and western basin walleyes during this time (Ferguson and Derksen 1971), the reduced populations with reduced mean age (Fig. 11) after the late 1950s may have contributed to the geographic isolation of the western and eastern basin stocks. The influence of the cooler environment on the adult stock as well as stock stability in the eastern basin are apparent from the continued presence of walleyes older than those in the western basin. Greater year-class variation, faster growth, and earlier maturity rates are characteristic of walleyes in the western basin. The walleye population in the New York waters of Lake Erie is a geographically discrete stock confined to the inshore waters of the eastern basin (Wolfert 1977; Wolfert and Van Meter 1978).

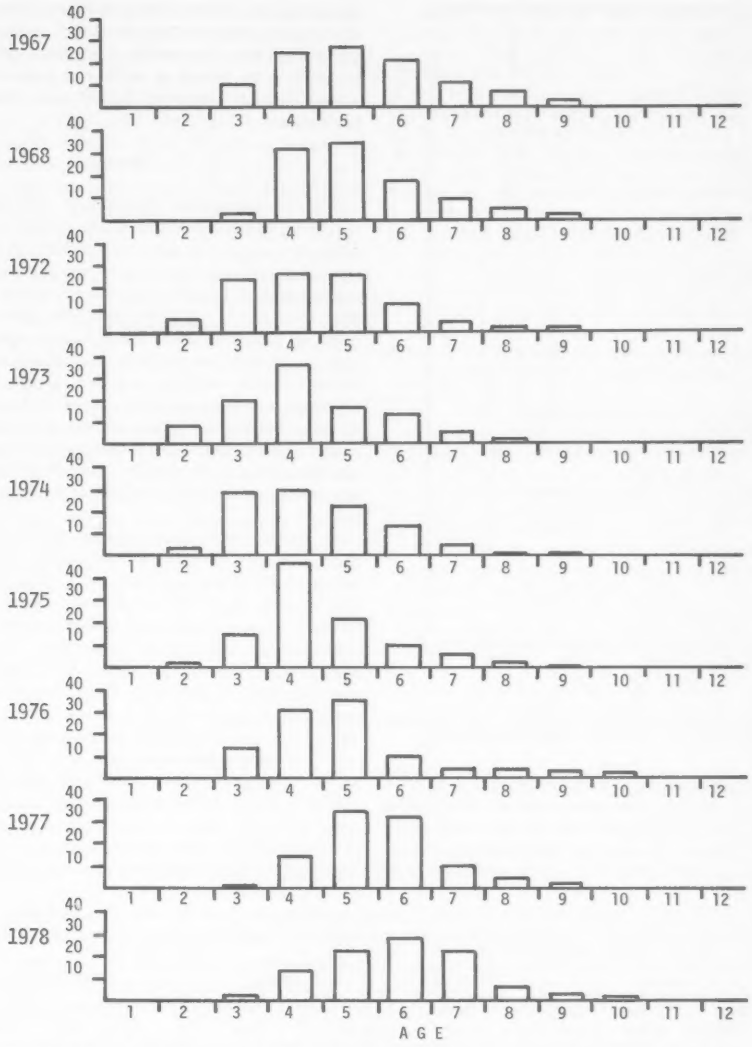

FIG. 10. Percentage frequency distribution of walleye in the angling fishery of Lake Nipissing during the open water season of 1967, 1968, and 1972–78. (Figure from Jorgensen 1979.)

A large spawning aggregation of walleyes is present in the Thames River, a tributary of Lake St. Clair. Postspawning migration from this location is to Lake St. Clair, St. Clair River, lower Lake Huron, and a small percentage to western Lake Erie (Ferguson and Derksen 1971). Mean age data from different locations in Lake St. Clair (Table 4) gives some indication of walleye subpopulations at Tremblay Creek and Mitchill Bay. The fall catch data from 1970 to 1979 is consistent for these two areas. Walleyes from Mitchill Bay with a larger mean age may be prespawning migrants from the St. Clair River and lower Lake Huron, while the younger ones at Tremblay Creek may be prespawning migrants from western Lake Erie or Lake St. Clair proper. The mean age of walleyes in Lake St. Clair has been increasing in recent years suggesting a buildup of the brood stock following closure of the fishery due to mercury contamination in the early 1970s (Table 4).

Slow-growing, late-maturing, and long-lived walleyes are very vulnerable to exploitation. The situations in Black Bay and Rainy Lake are a few examples of their vulnerability.

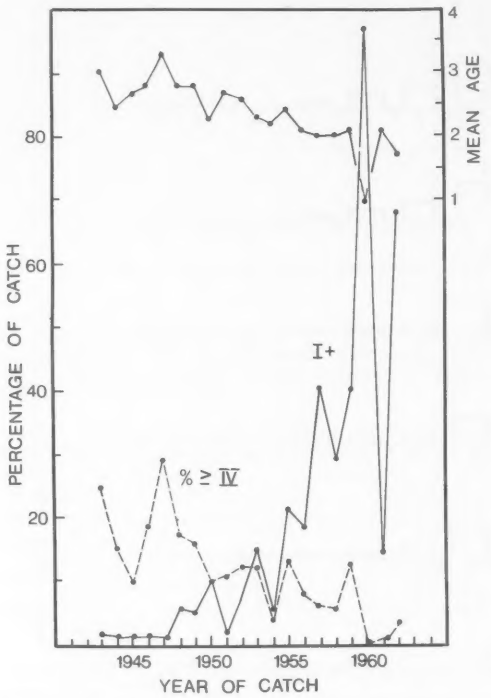

FIG. 11. Changes in the age structure of walleye from fall trap net catches in western Lake Erie, 1943–62. (After Parsons 1970.)

Another less documented case is the Chequamegon Bay stock on the south shore of Lake Superior (Swedburg and Selgeby 1978). In 1971 and 1972, court decisions involving native American fishing rights removed the legal obstacles which prevented commercial fishing for walleyes during their spawning runs into the Kakagon River, Wisconsin. In 1972, an intensive gillnet fishery developed and catches have declined since then. The decline of the Shoal Lake walleye stock in Lake of the Woods is another example of the effect of an unregulated, intensive fishery on a northern walleye population.

Models

Walleye populations respond to exploitation as self-regulating cybernetic systems. The degree to which a population can respond to negative feedback in the form of increased growth and earlier age to maturity depends on energy and nutrient availability. In northern climes where walleyes grow more slowly and mature later, the mean age of the catch must be greater to allow for adequate reproduction. Conversely, in more southerly regions where growth compensation is great, walleyes are able to mature much earlier following a decrease in density, as in western Lake Erie. We reviewed the changes in the mean age of several overexploited stocks and prepared a crisis curve suggesting the minimum age the catch can be reduced without collapsing the stock, depending on the energy available in the form of GDD > 5°C (Fig. 8).

In Black Bay, Lake Superior (GDD > 5°C = 1374), female walleyes probably did not mature until age 5 and did not reach 100% maturity until age 9 or older, depending on their compensatory reserve which was likely small (less than Savanne Lake, a warmer and shallower research lake located about 110 km northwest of Thunder Bay, Ontario). The mean age of the walleye stock in Black Bay dropped from 6.0 to 4.4 from 1966 to 1969 (Fig. 6). (C. A. Elsey, unpublished data). Had the mean age been retained above 5.0 and preferably at 5.5, we believe the population would have been saved and the fishery would have remained viable. The mean age of the walleye catch in the North Arm of Rainy Lake (GDD > 5°C = 1666) dropped from 5.3 in 1957 to 3.6 in 1967 and in the East Arm from 6.5 in 1955 to 4.4 in 1967 (Chevalier 1977). These stocks probably could have sustained much greater yields had the mean ages been held at 5.0 or

TABLE 4. Mean age of walleyes from various parts of western Lake Erie and Lake St. Clair, 1968–79. Data supplied by various agencies.

	Lake St. Clair – Thames River					Western Lake Erie								
	OMNR[a]				MICH DNR[b]	OMNR				OHIO DNR[c]			USFWS[d]	
	Fall Index		Thames	Summer	Spring	Creel Census		Comm. GN		Gillnet index			Comm. Trap	
Year	TC[e]	MB[f]	River	Creel[g]	Index[h]	I & II	IV	Spg.	Fall	Spg.	Sum.	Fall	Spg.	Fall
1968			4.38											
1969			4.72											
1970	2.53	4.46												
1971	2.90	4.50	5.95											
1972	3.07	4.48	5.52		4.75									
1973	3.68	4.69	4.65		4.11					2.01	1.57	1.91	2.97	
1974	4.65	5.35			5.34					3.04	1.29	1.66	3.05	1.76
1975	4.54	5.44			5.17	3.32	3.75			3.73	1.66	1.46	3.38	1.27
1976	5.44	5.92			4.63	2.36	2.74			2.33	1.80	2.00	2.69	1.46
1977	4.58	4.84		4.57	4.56	2.57	2.82			2.22	2.24	2.34	5.77	3.85
1978	3.50	4.94		4.21	5.68			3.22	1.69	1.93	1.82	1.67	3.37	1.27
1979	3.79	5.16						3.18	2.15	2.33	1.50	2.14	2.92	2.11

[a]Ontario Ministry of Natural Resources. [b]Michigan Department of Natural Resources. [c]Ohio Department of Natural Resources. [d]United States Fish and Wildlife Service. [e]Tremblay Creek. [f]Mitchill Bay. [g]Combined lake creel. [h]Mainly Anchor Bay.

above. In Shoal Lake (GDD > 5°C = 1642), Lake of the Woods, the walleye stock collapsed following heavy exploitation. During the decline, the mean age of the walleye catch dropped from 5.8 in 1962 to 3.4 in 1979 (Borecky 1979). In the Lake of the Woods, age at maturity for female walleyes was 5 or 6 (Carlander 1945) and presently is 5 (V. Macins, personal communication). Therefore, following the suggestions of Abrosov (1969), the mean age of the commercial catch of walleyes in that body of water should have been maintained above 5.0 to sustain the population and acceptable harvests. In Lake Nipissing (GDD > 5°C = 1746), with primarily an angling fishery but with a significant native subsistence fishery, the mean age of the catch dropped from 5.3 in 1967 to 4.2 in 1973 (Anthony and Jorgensen 1977). When restrictions were placed on the walleye harvest in 1975 to enable the brood stock to recover, the mean age of the catch rose to 5.9 in 1978 (Jorgensen 1979) and the possibility of the stock collapsing became less threatening.

In western Lake Erie, the mean age of the walleyes from the Ohio trap net catches was reduced to 2.7 at the time of large harvests (1943–54). Subsequently, the stock declined drastically (1955–62) and the mean age dropped to 2.0 (Parsons 1970). More recently, following the ban on fishing due to mercury contamination, the stock recovered and continues to build up under the present international management quota system. The combined weighted mean age of three separate walleye stocks tagged on spawning runs and subsequently recaptured by anglers (1975–77) was 3.46 (Van Vooren 1978), indicating that the brood stock is recovering in this area of Lake Erie. We suggest that maintaining the mean age around 3.0 would have been sufficient in this energy regime (2600 GDD > 5°C) to prevent the rapid decline in the stocks experienced during the 1955–62 period. Thus, we suggest that had the mean age of the catches for the various stocks been maintained above the proposed "crisis curve" (Fig. 8), most of these fisheries would exist today or at least would have continued to provide good walleye yields. Hopefully, no additional data points will become available in the future to verify further the validity of this assumed relationship.

If mean age of the catch, age to maturity, growth, and catch per unit effort are monitored, adequate information will be obtained to ensure that the necessary number of female walleyes are given an opportunity to spawn more than once, the number of years depending on the energy regime. Thus a sufficient number will survive to maintain adequate reproduction and avoid future collapse of walleye stocks.

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Genetic Identification of Sea Lamprey (*Petromyzon marinus*) Populations from the Lake Superior Basin[1,2]

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KRUEGER, C. C., AND G. R. SPANGLER. 1981. Genetic identification of sea lamprey (*Petromyzon marinus*) populations from the Lake Superior basin. Can. J. Fish. Aquat. Sci. 38: 1832–1837.

Sea lamprey (*Petromyzon marinus*) ammocoetes collected from 18 locations within Lake Superior were electrophoretically analyzed for genetic variability at 25 enzyme loci. Analysis by F statistics and χ^2 tests indicated that a significant degree of population structuring occurs among lampreys from Lake Superior. Cluster analysis of genetic distances generally grouped collections that were in close geographical proximity to each other. A weak but significant correlation was detected between genetic and geographic distances. It was concluded that multiple populations of sea lamprey occur within Lake Superior. If this is the case, then sea lamprey control emphasis might shift from individual streams to population regions to minimize the rate of reestablishment subsequent to chemical treatment. It may also be wise to avoid the planting of fish species with migratory habits so as to prevent the passive transport of adult lampreys out of their population areas.

Key words: lamprey, *Petromyzon*, genetics, population identification, Lake Superior, electrophoresis, management

KRUEGER, C. C., AND G. R. SPANGLER. 1981. Genetic identification of sea lamprey (*Petromyzon marinus*) populations from the Lake Superior basin. Can. J. Fish. Aquat. Sci. 38: 1832–1837.

Des ammocètes de grande lamproie marine (*Petromyzon marinus*) capturées à 18 endroits du lac Supérieur ont été analysées par électrophorèse en vue de détecter la variabilité génétique à 25 loci d'enzymes. L'analyse par statistique F et par tests de khi-carré montre qu'il existe, parmi les lamproies du lac Supérieur, un degré significatif de structuration de population. En général, le groupement des distances génétiques rassemble les sujets provenant d'endroits voisins. On a observé une corrélation faible mais significative entre les distances génétiques et les distances géographiques. Nous concluons qu'il existe plusieurs populations de grandes lamproies marines dans le lac Supérieur. Si tel est le cas, l'accent dans le contrôle de cette espèce pourrait être déplacé et passer de cours d'eau individuels à des régions de populations, de façon à minimiser le taux de rétablissement à la suite du traitement chimique. En outre, il serait sage d'éviter les peuplements d'espèces de poissons à mœurs migratrices qui favoriseraient le transport passif de lamproies adultes hors des limites de leur population.

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THIS paper proposes a population structure for sea lampreys in Lake Superior based on differences in allelic frequencies at allozyme loci among larval lampreys from 18 localities within the lake basin. The results of this study may have application for developing more effective lamprey control strategies.

The invasion, colonization, and population expansion of sea lampreys in Lake Superior during the 1940s and 1950s temporally corresponded to sharp declines in commercially important fish stocks, notably lake trout (*Salvelinus namaycush*) and lake whitefish (*Coregonus clupeaformis*) (Smith 1968; Lawrie and Rahrer 1972; Christie 1974; Pycha and King 1975). Much of this decline has been attributed to the predatory nature of sea lamprey adults, which cause mortality of prey fish through a process of attachment and feeding with a circular suctorial mouth. This predatory phase extends for 12–20 mo until the adult lampreys ascend tributary streams, spawn, and die. Larval lampreys (ammocoetes) remain in the tributaries for 3–11 yr or more before transformation and migration to the lake.

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An intensive management program to reduce the sea lamprey populations began in 1953 with the installation of electrical barriers in streams to block spawning runs (Lawrie 1970; Smith 1971; Smith et al. 1974; Smith and Tibbles 1980). Control measures became much more effective when the selective toxicants, TFM (3-trifluoromethyl-4-nitrophenol) and Bayer 73 (2′,5-dichloro-4′-nitrosalicylanilide) were used against the ammocoetes in streams. Application of these lampricides at intervals of 3–4 yr to Lake Superior tributaries continues to be the predominant tool used in sea lamprey control.

The control program is organized around a survey system that gathers data on the abundance of ammocoetes and the presence or absence of transforming lampreys in tributary streams. The basic management units for population control are thus individual streams known to harbor ammocoetes nearing the transformation life stage. The geographical correspondence between these streams and the populations in the lake itself is unknown. Adoption of a "stock concept management approach" (Loftus 1976) may increase the effectiveness of lamprey control.

Electrophoretic studies on lamprey population structure in the Atlantic coastal drainages and the Great Lakes have found the animals to be genetically distinguishable between widespread geographic localities. Brussard et al. (1981) found genetic distinctiveness among lampreys collected from the Finger Lakes of New York, Hudson River, Delaware River, Lake Ontario, and Lake Superior. Krueger (1980) determined that statistically significant genetic differences occurred among lampreys from Lake Superior, Oneida Lake, Lake Champlain, and the Bay of Fundy at one or more of four polymorphic allozyme loci. The present study was undertaken to determine whether genetically identifiable populations of sea lamprey have become established in Lake Superior. The geographical scope of this study is narrower than others since collections were taken from the drainages of a single lake basin.

Materials and Methods

Sea lamprey ammocoetes from 17 tributaries and one bay of Lake Superior were collected during chemical treatment or by electrofishing (Fig. 1). Animals from the Middle and Nebagamon rivers were transported alive and held in aquaria until just prior to analysis. The other specimens were frozen as soon as possible after collection and stored at −20°C.

Starch gel electrophoresis was conducted on lamprey muscle tissue according to the procedures given by Krueger (1980). The nomenclature for specifying enzymes, loci, and alleles is that proposed by Allendorf and Utter (1979). Gels were stained for 16 enzymes encoded by 25 gene loci (Table 1). Among these loci, four were demonstrably polymorphic; *AGP*, *MDH-1*, *PGI-2*, and *PGM-1*. Electrophoretic expression of ME and PER has been reported by Brussard et al. (1981); the remaining enzymes have been described by Krueger (1980). The buffer systems of Ridgway et al. (1970) and Whitt (1970) were used to resolve PER and ME, respectively.

The analysis of the genetic data followed the methods outlined by Avise and Felley (1979) and utilized inbreeding coefficients known as *F* statistics (Wright 1978). The fixation index F_{ij} was calculated for each collection (i) at each locus (j) using Levene's (1949) correction for small sample size. The mean fixation index per locus ($\bar{F}_{is}$) was calculated according to the procedures of Kirby (1975). The standardized genetic variance (F_{st}) was calculated as the ratio of the observed variance in allele frequency to the limiting value expected if the localities were completely isolated and fixed. The calculation of *F* statistics for the polyallelic *PGI-2* locus utilized a "synthetic" allele which represented the data from alleles *92* and *122* (see Eanes and Koehn 1978 for further discussion). For this analysis a locus was considered polymorphic in a population if the frequency of the common allele did not exceed 0.99.

Tests for departures from Hardy–Weinberg expectations at a locus (j) used χ^2 and were calculated as:

$$\chi^2_{ij} = F_{ij}^2 N_{ij}$$

where N_{ij} represents the number of lampreys analyzed from collection i and locus j. The overall heterogeneity χ^2 test between all collections at a locus (j) was calculated as:

$$\chi^2_j = 2 N_{\cdot j} F_{st}$$

where $N_{\cdot j}$ is the total number of fish analyzed at a locus (j). Other χ^2 tests of the genetic data followed that described by Snedecor and Cochran (1967).

The calculations of average heterozygosity per locus and its standard error were determined according to the procedures of Nei and Roychoudhury (1974). Genetic distances (Rogers 1972) were calculated for all pairs of collection locations based on the four polymorphic loci. The matrix of genetic distances was subjected to cluster analysis using the BMDP-1M program (Dixon and Brown 1979). Geographic distances between sample locations were measured as the shortest distances via lake shoreline. Environmental data for the collection locations were provided by the U.S. Fish and Wildlife Service and the Canada Department of Fisheries and Oceans. Spearman's rank correlation coefficient (Conover 1971) was computed to examine the relationships between genetic characteristics, geographical distance, and environmental variables.

Results

Genotypic frequencies within samples at the four polymorphic loci (*AGP*, *MDH-1*, *PGI-2*, and *PGM-1*) were close to Hardy–Weinberg expectations; of 64 comparisons only three deviated significantly ($P < 0.05$). The deviant comparisons occurred at *AGP* in collections from the Firesteel, Huron, and Nebagamon rivers. The fixation indices (F_{ij}) for these three collections were all positive indicating heterozygote deficiencies and suggests that population substructuring may occur at these locations (Wahlund 1928). A general trend towards heterozygote deficiency for all collections was indicated by the positive values for the mean fixation index ($\bar{F}_{is}$) at each locus (Table 2).

Allelic frequencies among collections were, in general, most similar within regions; the exception was the East Keweenaw region (Table 2). Lamprey from Washington Creek exhibited less genetic variability ($\bar{H} = 0.009$) than the

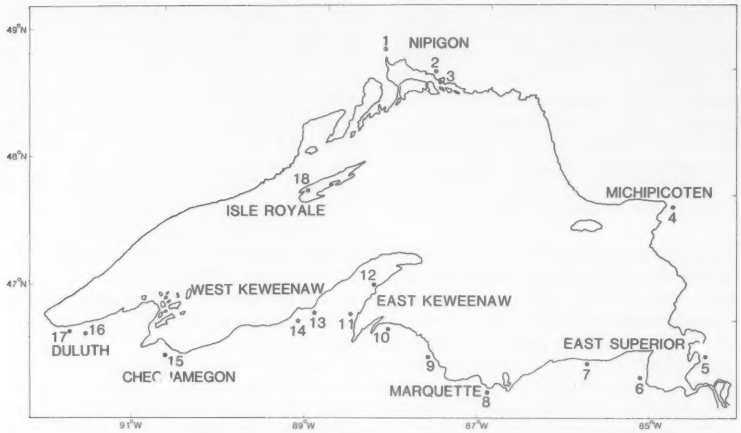

FIG. 1. Locations of sea lamprey ammocoete collections from the Lake Superior basin.

TABLE 1. Proteins, loci, and Enzyme Commission numbers used in this study.

Enzyme	Loci	EC number
Adenosine deaminase	*ADA-1,2*	3.5.4.4
Alpha-glycerophosphate dehydrogenase	*AGP*	1.1.1.8
Aspartate aminotransferase	*AAT-1,2*	2.6.1.1
Creatine phosphokinase	*CPK-1,2*	2.7.3.2
Glucose-6-phosphate dehydrogenase	*G6PDH*	1.1.1.49
Glyceraldehyde-3-phosphate dehydrogenase	*GAPDH-1,2*	1.2.1.12
Lactate dehydrogenase	*LDH*	1.1.1.27
Malate dehydrogenase	*MDH-1,2,3*	1.1.1.37
Malic enzyme	*ME*	1.1.1.40
Peptidase[a]	*PEP-1,2*	3.4.11
Peroxidase	*PER-1,2*	1.11.1.7
6-Phosphogluconate dehydrogenase	*6PGD*	1.1.1.44
Phosphoglucose isomerase	*PGI-1,2*	5.3.1.8
Phosphoglycerate kinase	*PGK*	2.7.2.3
Phosphoglucomutase	*PGM-1*	2.7.5.1
Sorbitol dehydrogenase	*SDH*	1.1.1.14

[a]Substrate: glycyl-L-leucine.

other samples (average $\overline{H} = 0.051$) and were unique in being fixed for the common alleles at *AGP* and *MDH-1* (Table 2).

The amount of genetic differentiation among collections relative to the limiting amount under complete fixation (F_{st}) was computed for each polymorphic locus (Table 2). F_{st} can assume values ranging from 0 (no differentiation) to 1 (maximum differentiation). The F_{st} values at different loci in this study varied from 0.02 to 0.06 with a mean of 0.04, which suggests some genetic differentiation between collections (Wright 1978). The F_{st} value calculated for lampreys are generally higher than those observed for bluegills (*Lepomis macrochirus*) within lakes in southeastern U.S. (Avise and Felley 1979; Felley and Avise 1980) and lower than those observed for Atlantic salmon (*Salmo salar*) from streams in Sweden (Ståhl 1981; see review of F_{st} values for other organisms in Selander and Kaufman 1975). The heterogeneity χ^2 values calculated from the F_{st} values indicated that significant genetic heterogeneity ($P < 0.05$) occurred at each locus among collections (Table 1; testing the null hypothesis that samples were drawn from a common population). It may be argued that the Washington Creek collection, with its reduced genetic variability, contributed solely to the large χ^2 values; however, highly significant differences ($P < 0.005$) remained at *MDH-1* and *PGM-1* when the heterogeneity tests were recalculated without these data. The above analysis indicates that a significant degree of population structuring occurs among lampreys from Lake Superior.

Genetic distances (Rogers 1972) were calculated between the sea lamprey collections to analyze further the population structure within Lake Superior. Cluster analysis of the genetic distances between the sea lamprey collections suggested a regional localization of lamprey populations (Fig. 2). Samples within regions usually formed discrete clusters, with the principal exception being the East Keweenaw collections. At genetic distances less than 0.06, five clusters were formed, representing collections from Nipigon, East Superior, Marquette–Chequamegon, Duluth, and West Keweenaw–East Keweenaw–Michipicoten.

Allelic frequencies and heterozygosities for each collection were compared to several environmental parameters (stream discharge, pH, total alkalinity, average summer water temperatures) and to the sea lamprey control histories of each locality. Using rank correlation coefficients, none of these variables appeared related to the genetics of the lamprey populations. A low but significant rank correlation did exist ($r = 0.18$, df = 134, $P < 0.05$) between genetic and geographic distances.

Discussion

The genetic data presented suggested that multiple populations of sea lamprey exist within localized areas of the Lake Superior basin. Although significant inter-region variability

TABLE 2. Allelic frequencies at four enzyme loci, average heterozygosity per locus, and *F*-statistics observed in sea lamprey collections from the Lake Superior basin (*$P < 0.05$, ***$P < 0.005$).

Collection location	*AGP*			*MDH-1*			*PGI-2*				*PGM-1*			$\bar{H}$	SE ($\bar{H}$)
	100	*146*	*n*	*−100*	*−165*	*n*	*100*	*92*	*122*	*n*	*100*	*148*	*n*		
Nipigon															
1 Nipigon River	0.54	0.46	39	0.79	0.21	39	0.97	0.03	0.0	39	0.56	0.44	39	0.055	0.030
2 Cypress River	0.48	0.52	25	0.76	0.24	25	1.0	0.0	0.0	25	0.50	0.50	25	0.055	0.030
3 Mountain Bay	0.50	0.50	18	0.75	0.25	18	0.97	0.0	0.03	18	0.56	0.44	18	0.057	0.030
Michipicoten															
4 Michipicoten River	0.65	0.35	40	0.81	0.19	40	1.0	0.0	0.0	40	0.70	0.30	40	0.047	0.027
East Superior															
5 Goulais River	0.60	0.40	29	0.87	0.13	40	1.0	0.0	0.0	40	0.50	0.50	39	0.048	0.028
6 Tahquamenon River	0.63	0.37	15	0.78	0.22	27	0.98	0.02	0.0	27	0.54	0.46	26	0.053	0.029
7 Sucker River	0.63	0.37	46	0.80	0.20	63	0.99	0.0	0.01	69	0.51	0.49	69	0.052	0.029
Marquette															
8 Au Train River	0.48	0.52	46	0.89	0.11	47	0.98	0.02	0.0	47	0.57	0.43	47	0.049	0.028
9 Big Garlic River	0.51	0.49	40	0.87	0.12	40	0.95	0.02	0.03	40	0.59	0.41	40	0.052	0.028
East Keweenaw															
10 Huron River	0.61	0.39	40	0.84	0.15	40	0.96	0.03	0.01	40	0.62	0.38	40	0.052	0.028
11 Sturgeon River	0.66	0.34	34	0.69	0.31	51	0.98	0.01	0.01	49	0.65	0.35	49	0.055	0.029
12 Traverse River	0.76	0.24	17	0.87	0.13	44	1.0	0.0	0.0	44	0.61	0.39	44	0.043	0.025
West Keweenaw															
13 Misery River	0.60	0.40	25	0.80	0.20	25	0.98	0.02	0.0	25	0.66	0.34	25	0.052	0.028
14 Firesteel River	0.60	0.40	81	0.78	0.22	81	0.96	0.04	0.0	81	0.67	0.33	81	0.052	0.028
Chequamegon															
15 Bad River	0.53	0.47	44	0.90	0.10	73	0.92	0.03	0.05	74	0.61	0.39	79	0.052	0.028
Duluth															
16 Nebagamon River[a]	0.67	0.33	41	0.86	0.14	62	0.98	0.02	0.0	70	0.77	0.23	42	0.043	0.024
17 Middle River	0.57	0.43	74	0.85	0.15	79	0.99	0.01	0.0	79	0.75	0.25	79	0.046	0.026
Isle Royale															
18 Washington Creek	1.0	0.0	44	1.0	0.0	69	1.0	0.0	0.0	60	0.87	0.13	63	0.009	0.009
F_{is}		0.036			0.018			0.135				0.025			
F_{st}		0.059			0.037			0.019				0.042			
Heterogeneity χ^2[b]		82.7***			63.1***			32.7*				69.7***			

[a]Data from Krueger (1980).
[b]Testing the null hypothesis that all samples were drawn from a common population.

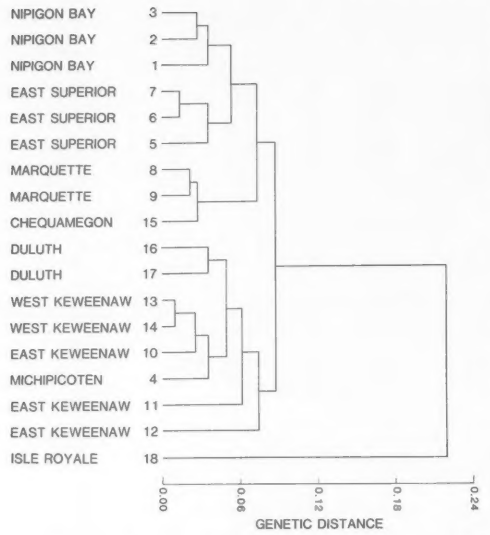

FIG. 2. Dendrogram generated by cluster analysis of Rogers (1972) genetic distance coefficients between collections of sea lamprey ammocoetes from the Lake Superior basin. Genetic distances were calculated using the data from the four polymorphic loci only. Collection locations are numbered according to Table 1.

in allelic frequencies was demonstrated, all alleles were distributed throughout the lake basin and the degree of inter-region differentiation was small.

Deterministic and/or stochastic processes, exclusive of long-term genetic differentiation, could have resulted in the establishment of the genetic heterogeneity observed among Lake Superior lampreys. Among the possible mechanisms that may have functioned are founding errors at initial colonization, transitory founding errors after chemical treatments, and selection.

Genetic differences may have become established through founding errors during initial colonization and are, perhaps, maintained by restricted dispersal from natal areas. If this is the case, subsequent mating or genetic exchange between regions would be limited. It is unlikely that such genetic differences would persist if lampreys freely intermingled and bred within the Lake Superior basin. Tagging studies in the Great Lakes have shown that lampreys are capable of traveling long distances (Applegate and Smith 1951; Smith and Elliot 1952; Moore et al. 1974). These studies, however, have not addressed the question of whether or not spawning runs in streams are comprised of adult lampreys with an admixture of natal origins. Recently, pheromones have been implicated as playing an important role in sea lamprey migration and reproductive behavior (Teeter 1980). The ability to detect trace quantities of chemical substances could facilitate the return of adults to natal streams. Irrespective of the mechanism preventing genetic exchange, the reduced genetic variability observed among lampreys from Washington Creek (Table 2) provides evidence that lampreys have not freely intermingled in Lake Superior. The invasion history of Washington Creek is exceptional from other localities in that lampreys did not colonize this stream until some time in the early 1970s (P. Rugen and R. Schuldt, Fish and Wildlife Service, Marquette, MI, personal communication). The probable physical or ecological barriers that occurred in this instance to prevent colonization and genetic exchange with other Lake Superior populations are unknown; however, the invasion history and genetic data suggest that such barriers have existed. The weak correlation between genetic and geographic distance suggests that some factor related to isolation by distance (Wright 1943) may be operative in preventing panmixia in the lake basin.

Alternatively, it might be argued that the genetic differences observed between sample sites are not stable attributes of populations but the transient results of founding errors from a general Lake Superior population repeated as often as each site is subjected to lamprey control treatments and subsequent recolonization. In this case, lampreys in streams geographically proximate could exhibit substantial genetic differences. This would seem to be a less likely explanation since genetic homogeneity occurred within each of the regions studied. Further investigations, however, are planned to study the temporal genetic variability among lampreys within a stream.

Selection is another possible mechanism that could be responsible for the genetic heterogeneity observed among lampreys. In the present study, no correlation was found between genetic and environmental variables. Correlative analyses, especially with so few variables, are insufficient for demonstrating that selection has occurred (Lewontin 1974). Thus selection remains as a possible mechanism for the results obtained, although we prefer the interpretation that uses founders effect and isolation by distances.

We believe that the regional genetic patterns described argue in favor of the existence of several populations in Lake Superior. If this is the case, then the adoption of a stock concept approach to management might allow an increase in control effectiveness. Control emphasis might then shift from individual streams to population regions. The basic management units for lamprey control would geographically correspond to population regions within the lake. Each of the streams located within a region, including minor lamprey producers, would be chemically treated simultaneously for several consecutive years. This management approach should decrease the probability for recolonization if adult dispersal from adjacent regions is limited. The prevention of passive forms of lamprey movement would reduce such dispersal and enhance population discreteness. It may even be wise to avoid planting fish species (e.g. Pacific salmon) that are known to have extensive migratory habits and which could serve as vectors for lamprey dispersal. The management strategies proposed should be experimentally examined for their control effectiveness before widespread implementation.

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Stock Identification: Materials and Methods[1,2]

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Various population parameters and physiological, behavioral, morphometric, meristic, calcareous, biochemical, and cytogenetic characters have been used to identify fish stocks. We define a stock as an intraspecific group of randomly mating individuals with temporal or spatial integrity. Each character set and the associated methodology relates to specific aspects of the stock definition. Population parameters are useful primarily for the recognition of putative stocks at the practical fisheries management level. Physiological and, to some degree, behavioral characters are used primarily to study differences in the adaptation of stocks to different environments. Behavioral characters are also important for the recognition of stocks and the study of their spatial and temporal discreteness. Morphological characters, including morphometric measurements, meristic counts, and the shape, size, and type of zonation in calcareous structures provide data that are useful for the precise description of and differentiation among stocks. Although the genetic control of this type of variation is poorly understood, multivariate methods coupled with shape analyses provide techniques that describe intraspecific subdivisions that have been found to correspond to genetic stock structure as determined by other methods. Intraspecific chromosomal variation has, on occasion, been employed for stock identification. This variation has had only limited application to the study of stocks because of complications arising from intraindividual variation and artifactual variation introduced by the methodology. Electrophoresis provides an important method for measuring the genetic discreteness of stocks and for the study of genetic relationships among stocks. Electrophoretic data have recently attained a primary position among the methods used for stock identification.

Key words: stock identification, genotype, phenotype, population parameters, marking, physiological, behavioral, morphometric, meristic, calcareous, cytogenetic, and biochemical characters

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On a fait appel, pour identifier les stocks de poissons, à divers paramètres de population et à des caractères physiologiques, éthologiques, morphométriques, méristiques, calcaires, biochimiques et cytogénétiques. Tel que nous le définissons, un stock est un groupe intraspécifique d'individus s'accouplant au hasard et conservant une intégrité spatiale et temporelle. Chaque caractère choisi et la méthodologie qui lui est associée se rapportent à des aspects spécifiques de la définition des stocks. Les paramètres de population sont surtout utiles dans l'identification de supposés stocks dans la gestion pratique des pêches. Les caractères physiologiques et, à un certain degré, les caractères éthologiques servent principalement à l'étude de différences dans l'adaptation des stocks à divers environnements. Les caractères éthologiques sont également importants pour identifier les stocks et étudier leur séparation spatiale et temporelle. Quant à la description précise des stocks et à leur différenciation, les caractères morphologiques, y compris mensurations morphométriques, numérations méristiques, et forme, taille et type de zones dans les structures calcaires fournissent d'utiles données. En dépit de notre pauvre compréhension du contrôle génétique de ce type de variation, des méthodes multidimensionnelles couplées à des analyses de forme permettent de décrire des subdivisions au sein des espèces, correspondant à la structure génétique des stocks, telle que déterminée par d'autres méthodes. À l'occasion, on s'est servi de la variation chromosomique intraspécifique pour identifier des stocks. Cette variation a eu toutefois une application limitée dans l'étude des stocks, à cause de complications résultant de la variation intra-individuelle et d'une variation artificielle introduite par la méthodologie. La séparation génétique des stocks, ainsi que l'étude des relations génétiques entre stocks peuvent faire appel à l'électrophorèse. Cette méthode occupe une place de plus en plus importante parmi les méthodes d'identification des stocks.

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THIS paper reviews some of the materials and methods that have been used to identify and discriminate among intraspecific groups of fish and to appraise their applicability within a stock definition. A wide variety of characters, ranging from population parameters to biochemical variation, is available for the study of intraspecific differentiation. Each type of character and the associated methodology pertains to distinct biological features of intraspecific groups of fish. Hence, the perception of stocks is very dependent on the character set with which they are observed.

Intraspecific groups of fish have been described by terms such as race, tribe, population, subpopulation, stock, and subspecies intended to reflect the magnitude of differences among such subdivisions. The term stock has been applied loosely (for a review, see Booke 1981), but generally implies some genetic contiguity among its members. A number of stock definitions have been proposed, ranging from those that emphasize the practical features of a stock as a production or management unit (Larkin 1972) to those that emphasize genetic discreteness (Ihssen 1977). For purposes of discussion for this paper, we define a stock as an intraspecific group of randomly mating individuals with temporal or spatial integrity. This definition characterizes an ideal or model stock that is, in practice, only approximated by intraspecific groups of fish that are commonly referred to as stocks. For example, production or management units of fish, differentiated on the basis of population parameters, are included as stocks under the definition even though the degree to which the conditions of random mating and temporal and spatial genetic integrity are satisfied is usually unknown. Hatchery strains are referred to as stocks even though they usually have limited temporal integrity and random mating is, at best, only approximated. The definition is useful because it provides a model against which observed supposed stocks can be compared. In fact, frequently it is the deviation from the definition (introgression, loss of temporal or spatial integrity, assortative mating) that is of interest to the manager.

This paper considers seven general types of materials and methods: population parameters, marking, physiological and behavioral characters, morphometric and meristic characters, calcareous characters, cytogenetic characters, and biochemical characters. The collection and analysis of each data type, as a rule, involves very different methodology and, therefore, each data type is treated separately in the subsequent discussion. Also, each data type applies differentially to specific aspects of the stock definition. Population parameters are frequently the characters by which sympatric stocks are initially recognized. The term sympatric stocks is used in this paper to denote stocks that are not isolated by physical barriers. Sampling for studies involving other characters is often on the basis of subdivisions within species recognized on the basis of population parameter differences. Physiological and behavioral characters have been used primarily to determine local adaptation of stocks and, hence, genetic differentiation among stocks. Morphometric, meristic, and calcareous characters are used primarily to study relationships among individuals within stocks and among stocks, such as stock membership, spatial distribution of stocks, and phylogeny of stocks. Biochemical techniques are especially useful and relatively new for the study of genetic

relationships among stocks, and their temporal and spatial genetic integrity.

Materials and Methods

Population Parameters

Included in this group are abundance, yield, age composition, growth, recruitment, and mortality, i.e. essentially the parameters which describe the dynamic properties of a population. These parameters are widely monitored by regulatory agencies concerned with allowable yields. In this connection, much has been written about their measurement and interpretation (Ricker 1975). Less well appreciated and described is the application of these parameters to stock recognition.

The test afforded by population parameters is one of spatial separation and is pertinent only with sympatric stocks. Allopatric stocks, by definition, occupy different geographic areas.

Because of their high sensitivity to extrinsic factors, population parameters tend to characterize the environment occupied by a stock as well as the stock itself. Members of a stock must respond in like manner to environmental conditions for this to be so, but such response is generally viewed as a stock attribute (Casselman et al. 1981). It follows that significant differences in population statistics between groups of fish can be accepted as evidence that different environments and, hence, different territories are occupied. Discreteness determined in this way may not be complete, and reproductive isolation is not necessarily implied for stocks so identified.

Genetic differences may increase or lessen phenotypic differences between stocks. In the first case, the result will be differences that are more discernable, and any conclusion reached concerning stock identity will be no less valid. In the second, any masking effect of genotype seldom will have much bearing on the outcome of a comparison because of the dominance of environmental effects. Density changes within a stock account for large fluctuations in growth. Stock size and physical factors contribute to changes in recruitment which are in orders of magnitude. Intense fishing shortens life span and prevents manifestation of inherent longevity in age structure. In contrast, the effects of genotype on these same parameters would be far more subtle.

In any test for sympatric stocks using population parameters, resolution will increase with the number of parameters included. Casselman et al. (1981) examined growth rate, age structure, and abundance (catch) trends in a study of sympatric lake whitefish (*Coregonus clupeaformis*) stocks in Lake Huron and were able to identify six stocks in addition to five others previously known from tagging. By assigning weights according to the perceived importance of the various parameters, they were able to represent the accumulated evidence for separate stocks numerically. Two of the lake whitefish stocks that they could discern inhabited contiguous basins within the same embayment and were less than 2 km apart. Resolution better than this is not to be expected from population parameters alone, and seldom will stock boundaries be so precisely defined.

Exploitation in most cases will enhance the usefulness of population criteria for stock identification by sharpening the distinction between stocks that otherwise might show close resemblances. Fishing is potentially one of the more severe stresses acting on fish populations and affects abundance, growth, age at first maturity, fecundity, recruitment, and survival (Regier and Loftus 1972; Spangler et al. 1977). Fishing tends, as well, to be more variable spatially than other physical factors which may affect sympatric stocks.

The characteristics of populations vary considerably in time as well as in space. Therefore, to the extent possible, temporal effects on sample variance should be minimized in any attempt to discern differences of spatial origin. Synchronous sampling across putative stocks included in any comparison is recommended. We also advise collecting data at times when temporal effects are least pronounced. For example, if length at age is chosen as a measure of growth, specimens should be collected between growing seasons.

Other sources of variance may confound comparisons unless precautions are taken. Unequal vulnerability of different sizes of fish to fishing gear is a source of error (Ricker 1975) that may be avoided by carefully matching gear in type, materials, and specifications. Segregation by age, size, or sex will interfere with attempts at representative sampling. Unsuspected cases, which will pose the greatest problem, may be safeguarded against by sampling during a period when the stock is likely to be homogeneous. For adult fish, the spawning period would be the logical time. Intermingling of stocks during periods of maximum dispersal is a further source of variation. Unless there is evidence to the contrary, one might assume, as did Casselman et al. (1981), that dispersal would be least at spawning times. The observations of Ihssen et al. (1981) would bear this out for lake whitefish. Sampling times should include the spawning period, then, if subsequent analysis reveals no seasonal differences in population statistics, the data can be combined.

The population parameter approach to stock identification has important advantages. One is the ease with which data are obtainable. The files of management agencies often will yield all that is necessary for a comparison of suspected stocks. Field sampling, if required, can be accomplished within a year and need not include independent fishing if there are established commercial or sport fisheries from which data can be secured. Second, the same data may be used to examine the status and stability of the stocks concerned. If the main thrust is to identify stocks as units of population for management purposes, the efficiency of this approach should not be overlooked.

Although population parameters have been examined for evidence of genetic selection (Ricker 1981), generally they provide no definitive information about the genetic character of a stock or its contribution to genetic variability. Nevertheless, simple recognition of a stock as a production unit may be important in a genetic sense, as management practices at the stock level will be conservative with respect to preserving genetic integrity.

Marking

Evidence of stock discreteness can also be obtained indirectly from marking studies. The conventional approach is to mark and release native fish in such a way as to permit

subsequent reidentification. Recoveries through time give point locations of fish from which the range and pattern of movement and, hence, degree of mixing among stocks may be inferred. Marking for this purpose has taken many forms including tagging, usually with serially numbered or coded tags, fin mutilation, branding, tattooing, and chemical or dye marking. One major problem associated with such studies is that it is difficult to tag a large proportion of the population, especially in stocks of commercial importance. Another drawback is that usually only a small percentage of the tagged animals are recovered (Ireland and Kanwisher 1978). However, the effectiveness of a tagging program can often be enhanced by a reward system where fishermen are paid for returning a tag with specific information on the site of recapture. For these reasons, marking may not be an effective tool in large systems, especially in terms of time and cost. Tagging studies have aided in the differentiation of stocks of lake trout (*Salvelinus namaycush*) in Lake Superior (Loftus 1958), lake whitefish in Lake Huron (Casselman et al. 1981), yellow walleye (*Stizostedion vitreum*) in Lake Erie and connected waters (Wolfert 1968; Ferguson and Derkson 1971), and herring in the northwestern Atlantic (Stobo et al. 1975).

Absolute abundance may also be determined by the mark–recapture method, using any one of a number of estimators (Ricker 1975; Seber 1973). Such information is of obvious value to managers, and also in defining population structure (Allendorf et al. 1981). The extrapolation of such estimates to large populations is less reliable, however, because the sample sizes are generally inadequate to meet the requirements for statistical validity.

Questions concerning gene flow between stocks can be addressed by marking studies, but it must be stressed that all stages of the life history should be followed. Marking of adults can answer the question of homing, and information suggesting how stock interactions may occur can be derived from investigations of spawning movements within the territory of a stock (MacLean et al. 1981). However, juvenile recruitment to the adult population is also critical in terms of defining genetic isolation. Intermingling that is revealed at certain times of the year may not lead to interbreeding if the tendency to home to specific spawning areas is strong (Horrall 1981). Thus, marking programs should ideally include some attempt to tag and recover fish on the spawning grounds, and then follow patterns of movement among larvae and juveniles. It should also be borne in mind that recovery locations and frequencies will largely be determined by the amount and distribution of the recovery gear deployed. This type of project on a large scale could foreseeably demand spatial and temporal coverage that would be both costly and time consuming.

Individual fish can be monitored more accurately using underwater acoustic biotelemetry (Ireland and Kanwisher 1978). A fish is equipped with an ultrasonic or radio transmitter which projects signals into the water, usually in all directions. These signals can be used to track an otherwise unrestrained individual for extended periods of time at ranges over 5 km (Stasko and Pincock 1977; Ireland and Kanwisher 1978). However, the use of this technique in stock identification is severely limited by the problems of tracking a large number of fish at any one time. Studies using dye-emitting tags (Leaman 1976) are similarly restricted in their application to stock identification.

In summary, the results of marking studies can provide invaluable information about movements to and from spawning areas, but are generally limited by the proportion of the population or stock that the tagged fish represent.

Fish can carry a number of natural marks that have been associated with stock differences. One of the most easily recognized and historically the first used was skin coloration (e.g. Goodier 1981). Another type of natural biological tag occurs in fish parasites. In some cases, parasites are stock specific either by species, abundance, or morphometric characteristics (e.g. Sinderman 1961; Nyman and Pippy 1972; Beverley-Burton and Pippy 1977; Pippy 1980).

Physiology and Behavior

Physiological and behavioral characters are closely associated with the fitness of individuals and stocks and, hence, are of particular significance to the practical application of the stock concept to fisheries management. The concept arose, in part, due to the recognition of within-species behavioral differences for reproduction and migration, and physiological differences for growth and fecundity (Ricker 1972; Loftus 1976). For example, among anadromous fishes individuals of the same species returning from the sea to spawn can frequently be separated into groups differing in time of river entry (called seasonal races (Berg 1959)), and for some freshwater species of fish individuals within the same lake can be separated into groups differing in rate of growth and maturation (Kennedy 1943; Beamish and Tsuyuki 1971). Within-species variation in reproductive behavior is of special interest because it frequently provides the isolating mechanism required for differentiation.

Physiological characters have been used primarily to study local adaptation of supposed stocks and, hence, genetic discreteness among stocks. Usually, stocks are compared for only one or a few characters. Behavioral characters, although also on occasion providing some insight into local adaptation, have been used primarily to study the discreteness of stocks.

Differences among stocks of fish for physiological and behavioral characters are more difficult to measure precisely than biochemical or even morphological characters because of their extreme environmental lability. For example, temperature tolerance is dependent on thermal history (Fry 1947), and spawning and migratory behavior can change substantially with environmental changes as is observed, for example, from transplantation experiments (Rupp and Redmond 1966; MacLean et al. 1981).

Physiological and behavioral differences among stocks and the relationship of these differences to adaptation have been investigated using two different approaches. One approach is to compare characters among stocks under controlled conditions in the laboratory or under partially controlled natural environments such as ponds and reservoirs. The second approach involves the study of stocks in their natural environments. Transplantation experiments are used to determine whether characters are habitat dependent. Ecological theory is used to test hypotheses regarding the adaptive significance of character differences observed among stocks.

For the first approach, the emphasis has been on determining whether, and to what extent, differences observed are

genetically determined. Sometimes physiological characters of samples collected from different supposed stocks are compared immediately after capture. For example, Bakhteyeva (1975) compared the cation concentration of the blood of spring and summer "races" of sockeye salmon (*Oncorhynchus nerka*) collected from different waters. Differences between the spring and summer races, as well as samples of the same race from different waters, were observed, and the author concluded that these differences are "inherent." Using similar methodology, stock differences in body composition have been observed for oil content of lake trout (Thurston 1962), serum phospholipids of sockeye and chum salmon (*Oncorhynchus keta*) (Akulin et al. 1975), and lipid composition of slender tuna (*Allothunnus fallai*) (Bishop et al. 1976). Although it is frequently postulated that such differences among stocks are genetic, it is recognized that they can be induced by environmental history such as feeding and temperature.

More usually, stocks are compared after acclimation to controlled laboratory conditions. A wide range of physiological and a few behavioral characters have been examined. G. W. Barlow (1961) found mean rates of oxygen consumption different among stocks of gobiids (*Gillichthys mirabilis*) after acclimation to laboratory conditions. The differences observed could be related to differences in the native environments these stocks occupy. Barlow interpreted these results to indicate genetic differences among these stocks for their metabolic response to temperature. Other studies, using similar methodology, have demonstrated differences among, for example, stocks of the spinous loach (*Cobitis taenia striata*) for respiration rate and enzymes associated with respiration (Minamori 1957, 1962), differences in temperature tolerance among stocks of various freshwater species of fish (Hart 1952; Morrissy 1973), differences in sodium efflux rate between stocks of seawater and freshwater medaka (*Oryzias latipes*) (Kado and Momo 1971), differences in temperature preference among stocks of white perch (*Morone americana*) (Hall et al. 1978), and differences in freezing point depression and Cl^- concentration among stocks of winter flounder (*Pseudopleuronectes americanus*) (Fletcher and Smith 1980).

Although many authors lean toward the interpretation that physiological differences among stocks observed after acclimation in the laboratory have a genetic basis, especially if these differences can be related to differences in the environments these stocks occupy, this is not necessarily the case. It has been shown that long-term acclimation, sometimes called acclimatization, can induce physiological changes that are irreversible by acclimation. This phenomenon has been called "irreversible nongenetic adaptation" (Kinne 1962). For example, Zamer and Mangum (1979) found, for clones of sea anemones, differences in rates of oxygen uptake, dependent on early environmental history, even after prolonged acclimation. Bradley (1978) found copepods raised at 20°C more tolerant to high temperatures than those raised at 10°C after acclimation to a common temperature, and Kinne (1962) found that fish derived from eggs reared at different salinities had different food conversion efficiencies. However, some physiological and behavioral characters may be completely reversible. For example, it was found for rainbow trout (*Salmo gairdneri*) (P. E. Ihssen unpublished data) that lots from the same families, incubated at different temperatures (3, 6, 9°C), had the same temperature tolerance after short-term acclimation (3–4 wk) when compared as fingerlings. Fry (1957) pointed out that physiological characters that are completely reversible by acclimation are more useful for the study of genetic stock differences than morphological characters, because morphological characters are usually not reversible by acclimation. In general, however, studies involving long- and short-term acclimation indicate that a necessary condition for determining that differences among stocks are genetic is that these stocks have identical environmental histories.

Usually, for studies of within-species physiological and behavioral variability complete control of environmental history is employed. Typically, such studies involve collecting eggs from different wild or captive stocks, artificial fertilization, and incubating and rearing under identical controlled conditions for the different supposed stocks. Differences among stocks that have been demonstrated using this approach include pH tolerance among stocks of brook trout (*Salvelinus fontinalis*) (Robinson et al. 1976; Swarts et al. 1978), growth rate, reproduction, and viability among stocks of carp (*Cyprinus carpio*) (Moav et al. 1974; Wohlfarth et al. 1975a), age of smoltification among stocks of Atlantic salmon (*Salmo salar*) (Refstie et al. 1977), and swimming stamina among stocks of brook trout (Green 1964). Examples of behavioral differences demonstrated by this methodology include migratory behavior between two stocks of rainbow trout (under wild conditions) (Neave 1944), upstream and downstream migratory behavior of sockeye salmon (Brannon 1967; Raleigh 1971), rainbow trout (Raleigh 1971), and cutthroat trout (*Salmo clarki*) (Bowler 1975), and "ability to escape seining" among stocks of carp (Wohlfarth et al. 1975b).

A further refinement of the technique to demonstrate genetic differences is the use of special crosses among the stocks to be compared, such as reciprocal hybrids and paternal and maternal half sibs. Eschmeyer and Phillips (1965) concluded from crossbreeding experiments between two stocks of lake trout that differ in lipid content that this character is "chiefly" genetically controlled; Bams (1976) concluded that return of pink salmon (*Oncorhynchus gorbuscha*) to their native stream is genetically controlled from a matched planting experiment of a donor stock and a hybrid between donor females and local males (he also noted a maternal effect for time of return). Bulger and Schultz (1979) found differences in heat and cold sensitivity among clones of *Poeciliopsis* hybrids. Reinitz et al. (1979) found differences in protein and ash content of rainbow trout stocks and their hybrids. Fraser (1981) found that one wild strain and the hybrid of this strain with a domestic strain generally survived better than a pure domestic strain of brook trout in small Precambrian Shield lakes.

The environmental history of the female parent may be a determining factor for character differences, even if the stocks are incubated and reared under identical conditions (Dentry and Lindsey 1978). When maternal and paternal half sibs were employed (Ihssen 1973; Refstie et al. 1977; Newkirk et al. 1977), strong maternal effects were sometimes observed. Newkirk et al. (1977) found that the salinity history of oyster eggs (females) affected their salinity tolerance. For some studies of stock differences, parents, as well as their progeny, had the same environmental history. For example, Ihssen and Tait (1974) found differences in swimbladder gas retention

between two stocks of lake trout that were parented from individuals incubated and reared under identical conditions in the laboratory; Thomas and Donahoo (1977) found differences in swimming stamina among stocks of rainbow trout derived from parents reared under the same hatchery conditions. Unless maternal half sibs derived from males of the stocks to be compared crossed to the same females can be employed (as was done for the Bams (1976) study), the environmental history of the parents, as well as the progeny to be compared, has to be controlled to demonstrate genetic effects unequivocally, especially for characters associated with early life history stages.

Laboratory studies of physiological and behavioral differences are frequently conducted to gain an understanding of differences in adaptation to diverse native environments of stocks. Extrapolating differences in characters observed under laboratory conditions to the wild environment, especially for characters associated with fitness, introduces the further complication of environmental–genetic interaction. Correlation between relative performance in the laboratory and differences in native habitats has been observed in a number of studies (e.g. Ihssen and Tait 1974; Kado and Momo 1971; Newkirk et al. 1977). Generally, however, the relative performance among a set of stocks may be very different under different environmental conditions. For example, Ayles (1975) found stock–lake interaction for growth and survival of rainbow trout; Moav et al. (1974) found that European carp showed a greater improvement with respect to reproduction and viability in "improved environments" than did other stocks of carp, whereas Chinese carp performed best under harsh conditions; and upstream and downstream migration behavioral differences between stocks of salmon and trout can be influenced substantially by changes in environmental conditions such as water source (Brannon 1967), temperature (Raleigh 1971), and rheotactic acclimation (Bowler 1975). Also, nonparallel performance has been observed in hatchery and wild environments, especially with respect to survival between stocks of wild and domesticated trout (Vincent 1960; Flick and Webster 1976). Hence, differences among stocks observed under one set of environmental conditions cannot generally be extrapolated to a different set of conditions.

Transplantation experiments are another approach to the study of stock differences. Such experiments have demonstrated the extreme environmental plasticity of physiological and behavioral characters. For example, growth rate (Rupp and Redmond 1966; Svärdson 1970), survival (Plosila 1977; Altukhov and Salmenkova 1981), and seasonal spawning time (Rupp and Redmond 1966; MacLean et al. 1981) are determined more by the habitat than the stock. Transplanted rainbow smelt (*Osmerus mordax*) that were stream spawners in their native habitat changed to shoal spawning in recipient lakes (Rupp and Redmond 1966). The latter study also found that maximum length and longevity were more lake than stock dependent. However, one stock retained its late season spawning habit when transplanted to a lake in which previous smelt populations had spawned earlier in the season. On the other hand, MacLean et al. (1981) found that the seasonal spawning time of transplanted lake trout stock changed by several weeks and became similar to the time of the native lake trout in the recipient lake, whereas Bams (1976) found that pink salmon, derived from transplanted eggs and local sperm, were significantly different from local fish in time of ocean return to the local stream. Hence, such physiological or behavioral life history characters can be habitat dependent or stock dependent in different habitats. Because such characters can have large environmental–genetic interaction components (Ayles 1975), and comparisons are made between only two habitats, native and recipient, precise conclusions regarding the genetic or environmental nature of such differences cannot be drawn.

Another approach to the study of stock differences is to compare the variation of a set of characters among more or less reproductively isolated intraspecific groups of fish occupying a broad range of environments. If the observed character variation is in accordance with adaptive ecological models (e.g. Beverton and Holt 1957; Murphy 1968; Schaffer 1974), then it is concluded that the observed differences are adaptive. For example, Schaffer and Elson (1975) compared life history characters of geographic stocks of Atlantic salmon. Mean age at first spawning was found to be correlated with several different measures of difficulty of upstream migration, such as distance. This correlation is predicted by ecological models developed by Schaffer (1974), based on optimum response of life history patterns to environmental variation. Hence, the authors concluded that these observed differences are adaptive. Similarly, Leggett and Carscadden (1978) compared life history characters of American shad (*Alosa sapidissima*) stocks and found that the proportion of repeat spawners was positively correlated with latitude of the home river and fecundity was negatively correlated with latitude. For harsher and more variable northern climates, a greater proportion of energy is allocated to migration than to each individual spawning. This results in better post-spawning survival and spreads the risk of high mortality of progeny for each spawning over more seasons in the more variable climates. These relationships are predicted by ecological theory on optimum allocation of energy resources to migration and reproduction (Beverton and Holt 1957; Schaffer 1974) and, hence, it is concluded that these character differences are adaptive. Power (1981) also noted variation in stock characters of Atlantic salmon of Quebec, Newfoundland, and Labrador consistent with the ecological models advanced by Schaffer.

The ecological approach to the study of within-species variation overcomes some of the difficulties associated with experiments that separate stocks from their native habitats. However, the drawback of this approach is that the range of characters, as well as environmental factors over which stocks can be compared, is much narrower than for controlled experiments. Under laboratory conditions, the range of an environmental factor such as temperature can be extended beyond the range usually experienced in the wild and, hence, differences in performance can be measured under critical conditions. Also, laboratory studies involving breeding experiments can give insight into the detailed genetic control of character differences and the response of such differences to environmental changes. However, as has been discussed, a parallel response among stocks between the controlled environment and their native habitats cannot be assumed because of environmental–genetic interactions. Nevertheless, the response of stocks to a broad range of environmental factors under controlled conditions gives a measure of differences in

the limits of adaptation of stocks to major features of the environment.

This discussion points out a fundamental dilemma in the application of the stock concept. Genetic differences among stocks for physiological and behavioral characters can only be measured by comparing stocks in the same environment, whereas the manager is primarily interested in the adaptation of different stocks to different environments.

Detailed life history information for intraspecific groups of fish may sometimes suffice for their management. Such management units may be defined as stocks, and whether they are genetically distinct may be of little consequence for some management decisions. However, to evaluate management options relating to the impact of major environmental changes, information is needed on the genetic discreteness of stocks. Options regarding, for example, the possible extinction of a stock (Maitland et al. 1981) or the genetic impact of exploitation (Ricker 1981) can only be evaluated if information on the genetics of stocks is available. Hence, the biological definition of a stock, including the condition of genetic discreteness, needs to be applied. In general, information gained from ecological studies (different stocks in different environments), as well as from experimental studies (different stocks in the same environment, the same stock in different environments), is required for effective management.

Morphometrics and Meristics

Anatomical characters have traditionally been used in ichthyology and fisheries biology to describe various categories of fish. Their application in stock identification, however, is complicated by the fact that phenotypic variation in these characters has not been directly related to particular differences in the genome (Clayton 1981). Moreover, the effects of physiological and epigenetic constraints on morphology in response to certain environmental parameters, such as temperature and oxygen, are poorly understood (Martin 1949; Gould 1977; Reidl 1978; Stanley 1979; Bock 1980; Todd et al. 1981).

This situation, confounded by an indistinct terminology, has often made it difficult to ascribe differences observed between samples of a species to particular stocks (Clayton 1981). In some studies, however, anatomical characters have indicated a stock structure similar to those obtained from alternative data (Henricson and Nyman 1975; Sharp et al. 1978; Berst et al. 1980; Casselman et al. 1981; Ihssen et al. 1981); thus their value in stock identification is warranted.

Morphological characters represent the synergism between shape and size, reducing the idea of form to a series of measured variables. If we consider that these data are an unnatural suppression of the biological form to the confines of a two-dimensional space, then it is clearly important which type of analysis is used to interpret the data. Moreover, the level of differentiation between stocks is likely to be more subtle than that commonly seen between most species of fish, and is also strongly affected by allometry (Huxley 1924; Gould 1966; Sweet 1980). The most appropriate analyses will, therefore, be those with a reduced susceptibility to spurious correlation while retaining the ability to detect small differences.

Debate as to the merits of ratios, regressions, scaling, and correlations (Mosiman 1970; Atchley 1978; Dodson 1978; Smith 1980; Thorpe 1980) has led many biologists to adopt multivariate procedures. A number of workers argue convincingly for the use of multivariate techniques (Blackith and Reyment 1971; Sprent 1972; Sneath and Sokal 1973; Brower et al. 1978; Albrecht 1980; Oxnard 1980). The point has also been made cogently that their use in anatomical studies is related to computational expediency rather than statistical applicability (Corrucini 1975). Quite clearly, the statistical assumptions of each method should be met; however, the robustness of procedures such as principal component analysis, discriminant function analysis, and factor analysis should not be underestimated. One warning note is that the complex calculations involved in these methods are often sufficiently removed from the final relationships that only apparent anomalies are detected.

The techniques given above have been used for stock separation in several species, including *Salmo salar* (Lear and Misra 1978; Riddell and Leggett 1981) capelin, (*Mallotus villosus*) (Sharp et al. 1978) Dolly Varden (*Salvelinus malma*) (Morrow 1980), and *Coregonus* spp. (Casselman et al. 1981; Ihssen et al. 1981; Todd et al. 1981). Advances in the application of other areas of mathematics such as Fourier biometrics and biorthogonal grid analysis (Younger and Ehrlich 1977; Bookstein 1978) now appear to have some potential for stock identification (Jarvis et al. 1978; Casselman et al. 1981). The main advantage of these two techniques is that they isolate shape differences more effectively than more traditional approaches.

Meristic characters generally include serially repeated elements such as numbers of fin rays or vertebrae. They are represented by discrete or noncontinuous data, which means that their predictive ability is likely to be less than that of continuous data (i.e. morphometric data); thus, the two types should clearly be treated separately in multivariate analyses. Moreover, experimental work on several species has shown that environmental factors such as temperature, salinity, pH, and oxygen tension can modify the expression of the genes responsible for meristic characters (e.g. Tåning 1952; Orska 1957; Lindsey 1964; Trojnar 1977; Dunham et al. 1979; Balon 1980; Todd et al. 1981; see reviews by C. W. Barlow 1961 and Fowler 1970). The number of serially repeated characters evidently alters with the environmental changes associated with latitude (e.g. Hubbs 1926; Tåning 1952; Gross 1977; McGlade 1981). Thus, the phenotypic expression of these characters represents a complex reciprocity between epigenetic, physiological, and environmental factors.

In certain studies, meristic characters provide evidence of stock structure that is concordant with other information; examples exist for the clupeids (Parrish and Saville 1965; Carscadden and Leggett 1975), engraulids (Marr 1957), coregonines (Lindsey 1961; Lindsey et al. 1970; Svärdson 1970; Todd and Smith 1980; Ihssen et al. 1981; Mann and McCart 1981), and salmonids (Ricker 1972; Berst et al. 1980; Martin and Olver 1980). The varied applicability of these characters for distinguishing between stocks is clearly a reflection of the fluctuating input of additive and nonadditive genetic factors. Thus, the major drawback to using both morphometric and meristic characters in stock discrimination is that few traits have been examined from a genetic standpoint: those that have include pyloric caeca (Bergot et al. 1981), vertebrae

(Tåning 1952; Orska 1957; Baxter 1958; Lindsey 1961), and body morphology and fin size (Riddell et al. 1981). Further laboratory and experimental work is needed to expand our knowledge of the genetic basis of morphological characters.

The points above relate specifically to stocks which are spatially or temporally separated; the situation under mixed conditions will of course be exacerbated. The problems given may thus become intractable and lead to the nonapplicability of anatomical characters for discerning stocks which are sampled during a mixed phase of their life history. However, many field biologists routinely measure some aspect of morphology and, in terms of costs, this type of information is certainly worth collecting if only to monitor changes in the species itself.

Calcified Structures

Scales of fish have been used for many years to identify individuals from specific areas, subpopulations, races, or stocks (see reviews by Krogius 1958; Major et al. 1972). Similarly, other calcified structures contain information which, if properly analyzed and interpreted, can be used to identify individuals. The study of calcified structures, both osseology (scales, calcified platelets; otoliths, calcareous accretions; and bones, acellular structures); and osteology (bones with cellular structure, containing osteocytes), provides valuable techniques for stock identification.

Although measurements and counts are made on calcified structures, their study should be treated separately from body morphometrics and meristics as traditionally practised (see Morphometrics and Meristics section). The analysis of calcified structures involves specific techniques, and the collection, preparation, interpretation, and analysis are specialized. Studies of calcified structures are different from those of body morphometrics in that measurements are made on a part, soft tissue is excluded, and form may be only a portion of the osseometric or osteometric study. A study of body meristics often includes lateral line scale counts, which have been successfully used to separate fish from different geographic areas (Svärdson 1952; McCart and Pepper 1971).

Scales are the calcified structures that have been used most frequently in these studies because they are the structures most often collected for routine age assessment. It follows that in extensive and detailed age interpretations, subtle differences among groups might be perceived. Usually no special preparation is required to detect these differences other than to magnify and examine the scale or its impressed image. However, it is essential that the samples being compared are from the same "key" or "preferred" scale sample area. This is especially important in studying and comparing archival collections.

The scale method of stock identification and assessment has been used to manage important fisheries units (e.g. Henry 1961). Scales have been examined to identify and discriminate among both marine and freshwater stocks that differ, for example, by geographic location, spawning season, or hatchery versus wild origin.

Several characteristics extracted from routine scale enumeration and mensuration have been used to identify single stocks and discriminate among mixed stocks. Scale ages have been used and involve an enumeration of annuli, usually in relation to a major environmental change frequently associated with migration (e.g. from river or stream to ocean or lake) (Clutter and Whitesel 1956; Mosher 1963; Major et al. 1972; Lear and Misra 1978; Biette et al. 1981). Scale sizes measured within and between zones have also been used to determine the origin and identification of fish stocks (e.g. Rowland 1969; Martin 1978). However, most frequently, the number and spacing of the circuli or sclerites in specific zones have been studied (Krogius 1958; Mosher 1963; Anas and Murai 1969; Tanaka et al. 1969; Bohn and Jensen 1971; Major et al. 1972; Lear and Misra 1978; Scarnecchia and Wagner 1980). Usually, the most detailed studies involved the use of a combination of these discriminating characteristics (see review by Major et al. 1972). The patterns of the circuli on the scales have also been useful, even though they probably reflect subtle physiological responses to specific environmental conditions. The characteristic configurations of the circuli in and about the annulus have alone been used to separate local stocks of northern pike (*Esox lucius*) (Casselman 1967) and sockeye salmon (Bugayev 1978). Scale shape has recently been used effectively to discriminate among sympatric fish stocks in the Great Lakes. This new method of quantifying shape by using Fourier series analysis has been used to identify and discriminate among stocks of yellow walleye (Jarvis et al. 1978) and lake whitefish (Casselman et al. 1981).

Studies of scale characteristics have succeeded in varying degrees, usually directly related to the detail of the data used in the analysis or the extent of isolation between the stocks. For example, Casselman et al. (1981) found that shape analysis correctly classified 59 to 86% ($\bar{x}$ = 73%) of the individuals of five stocks of sympatric whitefish from Lake Huron. In a similar study of the scales of six allopatric stocks of the same species, from 88 to 100% ($\bar{x}$ = 95%) of the individuals were correctly assigned to their respective groups (J. M. Casselman and R. S. Jarvis, State University of New York at Buffalo, Buffalo, NY., unpublished data).

Otoliths are also used for routine studies of age and growth and, as with scales, under detailed examination have been found to contain characteristics that are stock specific. In contrast with scales, otolith characteristics have been only recently, and less extensively, examined. However, similar features have been considered: age (McKern 1971; McKern et al. 1974); size, both length and weight (Rojo 1977); and type of zonation, including size and optical density of the nucleus (see review by Messieh 1972; McKern et al. 1974; Martin 1978). Messieh (1972) was able to identify Atlantic herring (*Clupea harengus*) stocks in the southern Gulf of St. Lawrence and adjacent waters using a rather qualitative shape analysis of the otolith. Otolith shape analysis, using planar shape quantification, has been used to discriminate among whitefish stocks from Lake Huron (Casselman et al. 1981).

Other bony structures have also been examined to differentiate among subspecific groups of fish. These osteological studies have not demonstrated conclusive differences. Gorshkov (1979) concluded that, in the cranium of chum salmon from three rivers in Asia, there were insufficient osteological differences to indicate segregation of subspecies. However, local populations were characterized by distinct, specific craniological features. Gasowska (1970) used cranial osteology to examine several forms of whitefish (*Coregonus*

lavaretus) from Poland, and concluded that the shape of the dentary was probably a good diagnostic feature but that there were no essential differences among the forms. From Gasowska's photographs of the dentaries, it is apparent that a more detailed shape analysis (e.g. Fourier series technique) would probably discriminate among these forms. With these structures, as with scales and particularly otoliths, stock identification and discrimination can be attained if the resolution of the analysis is great enough.

The characters in calcified structures are strongly influenced by environmental conditions, but a genetic basis exists, although it is more difficult to document. Some calcified structures, such as scales, are more strongly influenced by environmental conditions than are others, such as otoliths (Casselman 1978). This may explain why Casselman et al. (1981) found that otolith shape was a better discriminator than scale shape for whitefish stocks.

The chemical composition of scales has been used successfully to discriminate among various river stocks of salmon (Klokov and Frolenki 1970), and between anadromous and freshwater stocks of brown trout (*Salmo trutta*) (Bagenal et al. 1973) and whitefish (Moreau and Barbeau 1979). Scales of anadromous fish contain markedly more strontium. More sophisticated analytical techniques permitting greater resolution have been successfully applied to the problem, indicating that aquatic organisms and their calcified tissue possess a chemoprint, a form of natural chemical tag (Calaprice 1971; Calaprice et al. 1971). Although these techniques require specialized equipment, they should be more widely applied to the problem of stock identification.

Calcified structures also contain information that describes the behavior and physiology of the organism, both of which can be unique for a particular stock. If these structures are examined in detail, important characteristics, such as behavioral patterns associated with feeding (e.g. cycles) and specific temperature requirements (e.g. optima), can be detected. There are undoubtedly other features in fish calcified tissue that could be used in stock identification as more sophisticated qualitative and quantitative methods are applied to the problem.

Calcified structures are valuable tools in stock identification. They are especially useful because they are often collected for age and growth assessment and, for many analyses, require no special storage or preparation. They have the advantages that all the data are extracted from the one part, which does not deteriorate enough over time to affect most analyses and, in the case of scales, the fish need not be sacrificed. The analytical techniques can vary from those that are simple, practical, and easily incorporated into basic age and growth interpretation (e.g. scale analysis, Major et al. 1972) to complicated, costly, sophisticated technology (e.g. X-ray fluorescence spectrometry, Calaprice 1971). However, when systems are developed such that characteristics can be easily quantified, data collection can be mechanized and computerized, and the whole process can be rapidly performed, moderately cheap, and technically uncomplicated (e.g. shape analysis, Jarvis et al. 1978; Casselman et al. 1981).

A useful and relatively reliable method of validating the materials and methods of stock identification involves testing individuals classified as "unknown," but of known origin (e.g. Ihssen et al. 1981). However, in some cases this is not possible and other methods have been used. Anas and Murai (1969) reported that the results from the scale method they devised generally agreed with those from methods based on morphological characters. Tanaka et al. (1969) found that scale studies and tagging studies gave similar results for North American chum salmon. Messieh (1972) used relations of otolith length to fish length and fin ray count to validate otolith types (shape) as criteria for separating herring stocks. Bugayev (1978) used the presence or absence of an indicator parasite (*Diphyllobothrium* sp.) to assist in the development of criteria involving the convergence of circuli in the annuli of scales of sockeye salmon. Casselman et al. (1981) found that scale and otolith shape results were more similar to tag–recapture data, which indicated that each of the five stocks of Lake Huron whitefish was spatially separated and discrete, than to results and groupings for body morphometrics and meristics and electrophoresis. Shape analysis divided the five stocks into three groups whereas the other techniques placed them in only two groups.

Calcified structures and their analysis provide useful materials and methods for identifying and discriminating among stocks of fish and for assessing stock discreteness and interaction, even though their characteristics can be strongly influenced by environmental conditions.

Cytogenetics

The study of chromosome morphology and the behavior of chromosomes during meiosis and mitosis is called cytogenetics. Fish chromosome characterization (morphology) has been effectively done since 1945 (Booke 1968; Denton 1973), when refined cell and tissue culture techniques became available to permit resolution of the small size and great number of fish chromosomes, as compared with other vertebrate chromosome complements. As a result of these techniques, many fish karyotypes (the number and morphology of a species' chromosomes) have been described and it has recently become evident that besides fish species specificity of chromosome karyotypes, there is also intraindividual and intraspecific variation of chromosome morphology and number (Gold 1979).

Intraspecific chromosomal variation (morphology or number) can be useful for fish stock recognition. Ohno et al. (1965) and Becak et al. (1966) have demonstrated that rainbow trout and green sunfish (*Lepomis cyanellus*), respectively, can have intraindividual variation in chromosome number. Such variation has to be separated from intraspecific variation as noted in members of fish stocks. Intraspecific chromosomal number variation, for example, has been found generally throughout the superclass Pisces and particularly in the order Salmoniformes as follows: Atlantic hagfish (*Myxine glutinosa*) (Nygren and Jahnke 1972); *Salmo salar* (Roberts 1968, Barsiene 1978); *Salmo gairdneri* (Fukuoka 1972; Thorgaard 1976); golden trout (*Salmo aquabonita*) (Gold and Gall 1975); *Salmo clarki* (Gold et al. 1977); *Oncorhynchus keta* (Kulikova 1971); *Cobitis biwae* (Kobayasi 1976); goldfish (*Carassius auratus*) (Kobayasi et al. 1970, 1973; Arai and Fujiki 1977); *Mystus vittatus* (Manna and Prasad 1974); *Pseudobagrus aurantiacus* (Ueno 1974); stonecat (*Noturus flavus*) (Le Grande and Cavender 1980); Ozark madtom (*Noturus albater*) (LeGrande 1981); mosquitofish (*Gambusia*

affinis) (Cataudella and Sola 1977); blackstripe topminnow (*Fundulus notatus*) (Black and Howell 1978; Howell and Black 1981); *Etheostoma blennioides* (Ross 1973).

There are limitations to accepting intraspecific chromosomal variation as an indication of stock or population difference or integrity. We do not know whether such variation is the cause or effect of incipient speciation (White 1973) but, in any case, it appears to represent a stock genetic difference. The methodology for detecting chromosomal differences can introduce artifactual differences. Boothroyd (1959) and Rees (1967) have argued that most intraspecific chromosomal differences are due to errors in techniques rather than being true differences. We suggest that the following approaches be made before attempting to find a correlation between intraspecific chromosomal variation and stock recognition: (1) Examine 20 or more cells from the same organ in each fish specimen. Look at other tissue cells to differentiate between intraindividual versus intraspecific variation. (2) Look for dimorphic sexual chromosome differences that can be confounded as stock differences. (3) Look for polyploid cells that can be confounded as stock differences. (4) Look for possible cases of species hybridization versus true intraspecific variation. (5) Look at meiotic as well as mitotic tissue to observe chromosomal behavior. Postzygotic chromosomal variation will then be detected. (6) Take samples of at least 20 specimens from several locations to determine whether there is a geographic component to the possible chromosomal variation. (7) Compare the chromosome data to other data collected on as many characters (biochemical and morphological) as possible. (8) The newer techniques of chromosome banding (Howell and Black 1981) may also aid in detecting chromosome differences. By observing as many of these approaches as possible, true chromosomal variation will be detectable and may be a useful tool for stock recognition.

If these study approaches are followed, a considerable amount of time and effort will be encumbered. One person can require 3 days or more to determine each karyotype for each fish cell examined. A thorough chromosome study of fish in a watershed can depend on the number of sample locations and specimens taken, the number of cells and tissues examined, and the skill of the person using the chromosome techniques. We would conservatively estimate that a study can be completed in not less than 1 mo, and perhaps up to 12 mo, depending on all the variables mentioned. However, chromosomal computer scanning techniques (Green et al. 1980) show promise for increasing the speed for making comparisons between and among chromosome sets.

Electrophoresis

Electrophoretic data have led to a new era in understanding the genetic structures of a broad range of organisms including many species of fishes. The unique attributes of these data include capabilities of (1) using variants having a purely genetic basis, (2) measuring the individual contributions of up to (and sometimes exceeding) 50 loci, and (3) collecting substantial volumes of data with moderate efforts. These capabilities have opened new frontiers for investigations concerned with questions relating to stock discreteness and relationships. A previously lacking firm basis for quantification of relationships on the basis of purely genetic differences now exists. The resolving power of the method covers a taxonomic range from conspecific populations to different genera within a family. The prominent place of electrophoretic data in most of the background papers at this symposium (contrasted with its absence or peripheral place in similar gatherings prior to the 1970s) attests to the accelerated interest and legitimate use of electrophoretic data that has arisen during the past decade. Electrophoretic data have, therefore, shifted from an optional to a primary position among methods used in studies of discreteness and relationships among stocks. Some general properties of electrophoretic data, with regard to questions of stock identification, are outlined below. The reader is also referred to two recent books by Hartl (1980, 1981) for clear presentations of the basic principles of population genetics and the major role of electrophoretic data in current understandings of population structures.

Problems relating to single stocks — Electrophoretic data are useful for genetically characterizing individual stocks, based on allelic and genotypic frequencies. Data from at least 50 individuals and 20 loci are usually needed from individual collections for meaningful comparisons with data from other collections. Such data have reasonable confidence intervals around estimates of allelic frequencies, and they generally provide reliable estimates of average heterozygosity, a parameter which is useful for comparing levels of genetic variation among conspecific populations with data sets involving the same loci (see Allendorf and Utter 1979). Data from different collections, sampled over time or space, that have the same randomly distributed genotypic frequencies are consistent with a hypothesis that the samples are drawn from the same random breeding unit. However, such data are also consistent with other hypotheses such as limited gene flow or recent divergence (see Utter 1981).

Electrophoretically identified genetic characteristics of a relatively large and random breeding stock are temporally stable in the absence of immigration and differential fitness of allelic electrophoretic forms. This latter condition remains a subject of current debate. However, the levels of differential fitness originally anticipated, based on the sickle-cell model in man, have not been found among a large accumulation of empirical data. A null hypothesis of neutrality rather than selection appears to be the most reasonable expectation as a first approximation of reality when interpreting such sets of electrophoretic data as outlined above.

Nonrandom genotypic associations of alleles within loci (Hardy–Weinberg disequilibrium) or between loci ("linkage" disequilibrium) are positive evidence of nonrandom mating in a particular collection. A common cause of nonrandom genotypic distribution is the mixture of breeding units whose allelic and genotypic frequencies differ. These mixtures are typified by deficiencies in expected numbers of heterozygous individuals (under Hardy–Weinberg equilibrium) where allelic frequencies of one or more loci differ, and by nonrandom allelic associations between loci (i.e. linkage disequilibrium) where allelic frequencies of two or more loci differ. The sample sizes required for the detection of these associations vary according to the differences of allelic frequency of the loci involved. Nonrandom associations within a locus disappear following a single generation of random

mating. However, associations between loci persist following subsequent generations of random mating and decay at a maximum rate of 50% per generation between unlinked loci. Thus, studies of nonrandom allelic distribution between loci are useful for examining the possibility of recent admixtures.

Problems relating to mixed stocks — Many measures of population discreteness can be derived from electrophoretic data. As with variation within stocks, these measures depend on detection of polymorphism at one or more loci.

A simple and effective criterion for testing the genetic distinctness of two groups is consistently significant differences of allelic frequencies at one or more loci between samples from the two groups. A hierarchical sampling design is useful for partitioning variation into within- and among-group components. Analyses of data from such hierarchies identify population levels where structuring becomes evident and measure the distribution of genetic variation within a species.

Graphic representations of electrophoretic data can be useful for identifying distinctness and relationships among samples. Clustering of samples in such projections as dendrograms, trees, and principal components can clarify relationships by reducing complex data involving many variables into a simple visual image. The value of these methods must be tempered by a realization that some loss of precision is inevitable through the averaging that leads to the graphic picture, and that the projections are no more reliable than the data on which they are based. Relationships indicated by analyses of data from small samples, from only a few loci, from sets of data having dubious genetic interpretations, or from populations whose allelic frequencies have been perturbed by frequent bottlenecks are just as convincing to the uncritical eye as those reflecting more valid taxonomic entities. Nevertheless, similar interpretative constraints apply to clustering based on other types of data, and prudently interpreted electrophoretic data provide singularly valuable insights concerning relationships among both inter- and intra-specific taxa.

Reliable estimates of allelic frequencies, which reflect stable differences among stocks that intermingle during portions of their life histories, are a valuable data base for measuring the proportions of these stocks in mixed populations. Maximum likelihood estimates for proportions of contributing stocks can be obtained from known proportions of genotypes in mixed populations and in potentially contributing stocks. Meaningful estimates can be obtained from samples of 200 individuals where only moderate allelic frequency differences at nine loci distinguish the contributing stocks (Milner et al. 1981). This method of analysis is a powerful management tool for both wild and hatchery populations. It has distinct analytical capabilities and can be implemented at a relatively reasonable cost.

Genetic marking — Any stock having stable allelic frequencies at one or more loci that distinguish it from certain other stocks is genetically marked relative to these other stocks. As indicated above, this mark permits identification of this stock in the presence of the other stocks. The sample size required for the detection of different stocks in a mixed population depends on the amount of measurable genetic difference among component stocks and usually diminishes to single individuals between two stocks of distinct species. Naturally occurring differences among stocks may also be used to measure actual or potential interactions of native and introduced stocks (Clayton et al. 1971; Allendorf et al. 1980; Busack and Gall 1981; Wishard et al. 1981).

Although we have seen that these naturally occurring differences among stocks are useful, both for identifying discrete stocks and measuring compositions of stock mixtures, there are many instances where natural genetic differences are insufficient to make desired distinctions between two groups. Sufficient differences for such distinctions can be created by artificial breeding to intentionally alter allelic frequencies at individual loci. A requirement for intentional genetic marking may arise in such instances as when there is a need to identify individual fish and their descendents in experimental situations, or where measurements are needed of both long- and short-term effects of a particular hatchery stock on other populations. The concept has been suggested by several workers (e.g. Utter et al. 1966; Hedgecock et al. 1976; Allendorf and Utter 1979) and has been implemented in recent years as a tool in salmonid research and management (Crawford et al. 1978; Reisenbichler and McIntyre 1977; Schroder and Duker 1979; Seeb and Wishard 1977; Wishard 1980).

Genetic marking has some major advantages and unique capabilities. The mark is imposed at fertilization, marked fish are identifiable (as individuals or statistically, depending on the magnitude of difference between populations) throughout the ontogeny of a given generation, and the mark is passed on to succeeding generations. Thus, the mark not only exists at all life history stages of one generation, but also persists indefinitely as long as remnants of the marked population persist in an area. Such a mark (whether intentionally or incidentally present) is uniquely valuable in measuring reproductive success of individuals or populations and in following radiations over time of introduced populations into adjacent areas. Cost of intentional marking is moderate in the initial generation because the marked fish themselves do not require handling. Monitoring costs are negligible for marked brood stock.

IMMUNOGENETICS

Immunogenetic methods are currently of historical rather than practical importance in the study and management of fish stocks. An advocacy and application of these methods arose during the 1950s in response to their successful applications in anthropological studies (see Cushing 1956; Ridgway and Klontz 1960). Some applications of immunological methods relative to fish stocks have been made (reviewed in deLigny 1969) and limited use persists (Altukhov 1974). However, technical problems such as erythrocyte and reagent instabilities, and questionable genetic bases (reviewed in Hodgins 1972), coupled with the maturation of electrophoretic methods have led to a virtual abandonment of immunological methods as a practical tool in applied populations genetics relative to fish stocks. Electrophoretic methods are a vastly more effective means for obtaining data on genetic variations of fish populations (see Utter et al. 1974) and have now achieved the goals originally envisioned for immunogenetic methods.

Discussion and Conclusions

From the previous discussion of individual data types, one can see that each type pertains to only specific aspects of the total character of a stock. Population parameters are useful primarily for the recognition of putative sympatric stocks. The data are used mainly to manage production units. However, because population parameters in themselves do not tell us anything about the genetic discreteness or local adaptation of stocks, they severely limit the range of effective management decisions that can be taken solely on the basis of these characters. No decisions regarding the need of protection from extinction of such management units can be made on the basis of this type of data, except the most conservative decision to protect all such subgroups equally. Such a management procedure is usually not practical. Considering additional data types may provide the information required for the more efficient management of such subgroups.

Marking data have been useful for determining the spatial discreteness of stocks and for estimating the size of stocks. Sometimes tagging data have been used to attempt to estimate gene flow between stocks. However, it is difficult or impossible in most cases to show that fish movement and behavior are correlated with gene flow. Tagging data may only be measuring movement rather than gene flow. More sophisticated electronic tags that can transmit physiological functions as well as location of individuals may provide a tool for determining whether migrants actually interbreed with the nonnative stock with which they have been observed (by simpler tagging methods) to aggregate during spawning times. If specific biochemical genotypes (see Electrophoresis section) can be bred into a stock, gene flow between stocks can be estimated more directly.

Physiological and behavioral characters have been used to determine local adaptation of stocks. Such studies frequently involve estimating the degree of genetic control of character differences among stocks. The methodology for measuring such genetic differences is difficult, especially if differences with respect to native habitats are to be measured, because of acclimatization effects and environmental–genetic interaction. Usually differences in adaptation among stocks to their respective environments can only be inferred, rather than unequivocally demonstrated. Nevertheless, studies of such character differences have sometimes convincingly demonstrated that within-species subgroups of fish are differently adapted to different habitats. In the Great Lakes context, a better understanding of the nature and extent of local adaptation of stocks of whitefish and lake trout, for example, is required for management decisions regarding conservation and rehabilitation.

Morphometric, meristic, and calcareous characters are potentially powerful for measuring discreteness and relationships among stocks. The major limitation to their wider application for the study of intraspecific genetic differentiation is our ignorance of the heritability of the morphological variation. In this regard, morphological characters are similar to physiological characters. However, physiological character differences that are environmentally induced can sometimes be reversed by acclimation, whereas this is not the case for most morphological characters. To determine the degree of genetic control of morphological variation, breeding studies under controlled environmental conditions are required. As was discussed for physiological characters, such studies involve the same difficulties, but to a lesser degree, with respect to relating the results from experiments under laboratory conditions to the natural environment.

For morphometric, meristic, and calcareous characters, in contrast with physiological and especially behavioral characters, a large number of variables can be obtained from each individual. On the basis of such large volumes of multivariate data, individual stocks can be accurately characterized. The stock membership of individual fish can be precisely determined (e.g. Ihssen et al. 1981). However, relating this detailed morphological characterization to local adaptation has been possible only rarely (e.g. Riddell and Leggett 1981). If relationships between these variables and local adaptation could be established, morphometrics would provide an even more useful method for the management application of the stock concept.

Calcareous structures contain information which in many ways is similar to that obtained from body morphometrics and meristics. Although their characteristics are strongly influenced by environmental conditions, and genetic integrity cannot be assessed, this does not prevent them from being valuable tools which have been widely and successfully used to recognize and manage fish stocks (e.g. Henry 1961; Major et al. 1972). In addition, calcified structures provide important morphological, physiological, and behavioral data. The application of this material to the problem of stock identification is especially useful as these structures are often routinely collected and interpreted for age and growth assessment. These materials and methods permit a very practical approach to the problem. The samples are easily collected and stored and data extraction can range from simple to extremely complex and from manual to mechanized, depending on the expertise and equipment available. They possess the added advantage that sampling and data extraction need not be consumptive either of fish (e.g. scales) or materials (e.g. shape analysis).

Chromosome morphology is representative of genotype because it is largely unaffected by the environment and, hence, can be used to identify stocks of fish if sampling precautions are observed. The present means of studying chromosomal morphology are time consuming, but these methods may be productive if other characters available for study are limited.

Protein variability, as determined by gel electrophoresis, is unique among the data types discussed here because phenotypic expression is virtually unaffected by environmental variation and, hence, is the only kind of data that measures genetic differences among stocks directly. Therefore, electrophoresis provides a tool for measuring temporal and spatial genetic discreteness of stocks. However, as pointed out by Utter (1981), it is entirely possible that stocks are electrophoretically indistinguishable but, nevertheless, adapted differently to their respective environments (Kirkpatrick and Selander 1979). Hence, an observed electrophoretic difference is a sufficient but not necessary condition for two groups of fish to be genetically differentiated.

Attempts have been made to establish relationships between isozyme variation and physiological function with

varying results (e.g. Moon and Hochachka 1971; Wilson et al. 1973; Tsuyuki and Williscroft 1973; Hochachka and Clayton-Hochachka 1973; Brown 1977). Correlations between enzyme polymorphisms and physiological character variation have been demonstrated (e.g. Reinitz 1977) but the causal relationship between these two types of variation suggested by some authors has been questioned by others (see Brown 1977; Allendorf and Utter 1979). Some studies have demonstrated electrophoretic allele frequencies temporally and spatially correlated with environmental variables (e.g. Johnson 1971; Hedrick et al. 1976; Koehn et al. 1976). However, as Allendorf and Utter (1979) have pointed out, such correlations are predicted by random drift models that assume the selective neutrality of isozyme variation (Kimura and Maruyama 1971). Other studies have taken the argument one step further and demonstrated correlation between geographic clines of isozyme frequencies and in vitro functional differences among such isozymes (e.g. Merritt 1972). But, as has been suggested by Brown (1977), in vivo differences in the biochemical action of isozymes need to be determined "to demonstrate a selective basis for enzyme polymorphisms." Then, if such isozymes are found to vary in frequencies among stocks, in accordance with environmental variables that affect their functional optima, a convincing case will have been made for the adaptive interpretation of the enzyme variation.

Some studies have concluded that the observed variation in isozyme frequencies can be accounted for by a model assuming selective neutrality of this isozyme variation, coupled with random genetic drift (e.g. Aspinwall 1974; Sarich 1977). The selectionist versus neutrality interpretation of this type of genetic variation has not been resolved. For the practical application of electrophoretic data, it is frequently assumed as a first approximation that such variation is selectively neutral (Utter 1981). If it should be shown that the fitness effect of enzyme variation has been underestimated, and if it should become possible to relate electrophoretic differences to differences in local adaptation, then electrophoresis would provide an even more important method for the understanding of within-species genetic variation. Because electrophoresis can easily measure variation for large numbers of individuals and loci, it would provide a more efficient method for determining differences in local adaptation than the direct observation of fitness characters that are more difficult to measure.

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Community Consequences of Fish Stock Diversity[1,2]

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Genotypes are variable among fish stocks, and these limit potential niche. In turn, realized niche is further constrained by the interaction of abiotic and biotic environmental factors, together with fishery exploitation. Selection pressures by these three factors provide feedback on genotypes, modifying potential niches. The steady-state consequence of this process is a harmonic community of co-evolved stocks. Using community size structure as one of our criteria, we trace the effects of the major classes of perturbation on harmonic communities, and discuss their management implications.

Key words: harmonic community, co-evolution, fish stock, management, genetics, biotic and abiotic environmental factors, niche

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Les stocks de poissons renferment des génotypes variables, ce qui a pour effet d'imposer des limites à une niche potentielle. Une niche actuellement occupée est en retour davantage limitée par l'interaction de facteurs abiotiques et biotiques, ainsi que par la pêche. Les pressions de sélection exercées par ces trois facteurs agissent par rétroaction sur les génotypes, modifiant les niches potentielles. L'équilibre résultant de ce processus mène à une communauté harmonique de stocks qui ont évolué ensemble. Utilisant la structure par taille de la communauté comme un de nos critères, nous suivons les effets des principales classes de perturbations sur des communautés harmoniques et en examinons les implications pour la gestion.

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RECENT advances in ecological theory prepare the way for considering comprehensive approaches to the management of fish communities. An understanding of the implications of recent discoveries in fishery genetics provides the fishery manager with the tools necessary to bridge the gap through phenotypic expression and niche fundamentals to the concepts of natural, co-evolutionary, harmonic communities of fishes comprised of diverse, genetically distinguishable stocks. The necessity for maintaining harmonic fish communities appropriate to the corresponding environment in which their co-evolution occurred is related to fundamental precepts of ecology and stems from even more basic genetic principles. Appropriate management of Great Lakes fish stocks therefore depends on a thoughtful melding of genetic knowledge with ecological understanding, applied to the complex biological problems which themselves contain social and economic elements. Accordingly, we propose a concept and a methodology for the future management of Great Lakes fish stocks based on current genetic and ecological knowledge, with consideration of some social and economic contexts.

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Concepts

THE COMMUNITY NICHE

The inherent importance of genetic diversity over space and

time is its contribution to the survival of organisms, through the adaptation and optimization of their capacities to respond to a variable and varying environment. The ecological niche of an organism provides a useful measure of its response capacity, relative to the abiotic (temperature, O_2, pH, etc.) and biotic (competition, predation, etc.) factors that comprise its total environment. This is a physiological definition described in detail elsewhere (Kerr 1974a; Kerr and Ryder 1977; Kerr 1980). In essence, it embeds the physiological concepts of Fry (1947) within the n-dimensional niche structure of Hutchinson (1957). Specifically, the potential physiological niche is a hyperspace (equivalent to the fundamental niche of Hutchinson) which describes a genetically determined potential that is characteristic of an organism, and in which each environmental dimension provides an operational limit on metabolic scope for activity (Fry 1947).

Biotic factors, characteristic of any particular community, further restrict expression of full genetic potential. Thus, predation, competition, parasitism, or food web and spawning interactions, to name but a few, further constrain the potential or fundamental niche to a reduced hyperspace or realized niche. The realized niche is a most important consideration at the stock level because it is jointly determined by the genetic delineation of fundamental niche potential, as modified by the aggregate effects of all environmental factors. The functional concept of niche is equally applicable to stocks or species. Quantitative, time-dependent differences may exist, however, in the formation of characteristic niches for stocks or species, due to differential rates of gene flow.

The community niche may be considered to be the consequence, through interaction at the niche interfaces, among all the realized niches of the component fish stocks as well as all of the associated biota. Gartner-Kepkay et al. (1980) have clearly shown that basic demographic parameters such as growth and mortality rates of different stocks of a given species are genetically adapted to specific habitats. It would be expected then, that a community of organisms which had evolved over many generations would ultimately be closely attuned to its environment, the component stocks of organisms approximately coordinated through their mutually interacting niche boundaries, and comprising a harmonic community (Ryder and Kerr 1978). Long co-evolution leads to niche packing, which results from adaptive response of organisms to their community associates. Competition for niche space and a gradual but continual oscillatory damping of niche interactions results in a steady-state or harmonic community. Harmonic communities become suited to survival in a specific environment in response to genetic shifts and appropriate phenotypic responses to the temporal and spatial variability of all biotic and abiotic environmental factors.

Because they are derived from niche packing, harmonic communities possess an ecological advantage over astatic aggregations of organisms (Ryder and Kerr 1978) that result from exogenous cultural stresses such as exploitation, environmental degradation, or introduction of or invasion by exotic species (Loftus and Regier 1972). The advantage gained through the long-term co-evolution of the internal components of harmonic communities would seem to be in the optimization of their genetic resources for maximum efficiency in exploitation of their environment. The beneficial

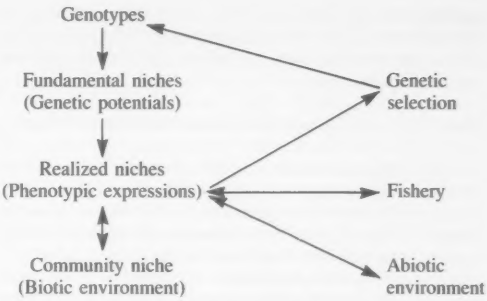

FIG. 1. Depiction of the major elements of fish production systems, showing that the genetic potential of the constituent genotypes is realized in the form of phenotypic expressions affected by three major sources of influence: the biotic and abiotic environments, and fishery effects. The major feedback pathway is via reproduction, which affects subsequent genetic potential through genetic selection in response to the three major sources of influence. For further amplification, see text.

output of niche packing, from an anthropocentric point of view, is a community of fish stocks utilizing its environment efficiently (Dobzhansky 1951).

Any modification of a harmonic fish community may be seen as a departure from the optimal condition and therefore is associated with a reduction in quantity, quality, and predictability of the ecosystem or subsystem output. It is, of course, recognized that natural communities may not be in perfect and sustained dynamical equilibrium. Fluctuations in abiotic conditions may result in changes in relative abundance of various stocks. The biotic interrelations may be characterized by periodic oscillations in abundance. Whatever their source, fluctuations in abundance of component stocks may also be viewed as part of the machinery of adjustment of a harmonic community. To summarize, three major classes of factors shape community structure: internal community dynamics, abiotic environmental variation, and fishery selection (Fig. 1). In concert, these factors determine the forms of the individual realized niches, which in turn may generate selection pressures to modify genetic potential.

Concomitantly, we draw on several abstract ideas to support our comprehension of harmonic communities. Besides those concepts to which we have already alluded, we invoke current ecological conceptions of trophodynamics, particle-size spectra, size-selective and optimal foraging, stability and resilience, population genetics, biogeography, domination and dependence principles, morphoedaphic considerations, hierarchic levels of approach, $r-K$ selection spectra, salmonid phenotypic plasticity, photosynthetic strategies of algae, turnover rates, taxocene dynamics, rehabilitation strategies, interactive segregation, and adaptive responses of fish associations to cultural stresses. Taken together, these concepts contribute to our overall understanding of harmonic communities, although it is beyond the intent of this contribution to attempt an integration in detail of these various ideas. In each instance, however, we cite references that provide entry to the relevant detail available in the ecological literature.

Given this view of the interactions of stocks with their

aggregate environment, it is useful to consider what forms of displacement may result from stock perturbations, and whether characteristic behaviors emerge that can be used to describe integral communities.

Structure and Dynamics of Harmonic Communities

Undisturbed and unharvested fish production systems comprise harmonic communities of co-adapted stocks, and perturbation of the stock balance can be expected to have the potential for ramifying effects throughout the system. A basic question emerges with respect to the possibilities for generalized descriptions of perturbation effects: do harmonic communities exhibit structural conservatisms, or displacement dynamics, that are characteristic of a wide variety of perturbation types, or must each instance be analyzed in an *ad hoc* manner? We believe there is ample evidence for the existence of generalized community behaviors that may be useful as guides for management.

If a community is described in terms of some given location in the hyperspace generated by the parameters of its community niche, one important consideration is whether a displacement of given magnitude will result in a smooth return to dynamical equilibrium or, alternatively, in an abrupt transformation to a new location in niche space. Abrupt transformations appear to be relatively common in the Great Lakes and similar fish communities (Holling 1973; Kerr 1977), indicating that both types of community dynamics are possible. It appears that community dynamics are appropriately described in terms of smooth transitions for small perturbations that do not displace the system from a stable basis of community niche space, but by rapid transformations among a possible multiplicity of stable configurations as critical parameter values are exceeded. It is of considerable interest to be able to predict when sudden transformations or bifurcations are likely to occur in response to changes in some system component.

Various properties of ecological system description can serve to complicate community analysis. For example, Poole (1978) examined the generalized behaviors of populations comprising a number of interacting subpopulations. For present purposes we may regard the latter as "stocks," potentially differing in terms of characteristics such as, say, timing of reproduction. Poole reached several conclusions, of which two are of interest here. First is the "domination principle," i.e. that the behavior of the population as a whole is predominantly determined by the most variable of its component stocks. Even a slight change in variability of one stock can disproportionately affect the whole population. Second is Poole's "dependence principle," i.e. that population behavior is not simply the sum of the individual stock characteristics, but can be strongly affected both by interaction among stocks and by differences in timing in relation to environmental variables of various stocks. Consequently, aggregate population behavior is not simply predictable on the basis of stock–environment interaction, but depends heavily on the geographic scale of definition of the stock assembly. In particular, the appearance of population stability can be as much determined by different phasing among stocks as by the inherent variability of the stocks themselves. An appropriate example of this kind of thinking may be exhibited by Pacific salmon. It may be speculated that all of the stocks of, say, sockeye salmon (*Oncorhynchus nerka*) on both sides of the North Pacific Ocean comprise a single population (in the sense of Poole) that is divided into many stocks that mutually share the oceanic grazing resources by devices that involve both spatial and temporal differences. The abundance of those stocks which spawn, for example, in Canada, may suggest a great variability in population size, but if these fluctuations are compensated by fluctuations in stocks of Alaska and Asia, what emerges is a picture of population stability in the North Pacific as a whole.

In terms of stability or displacement of the whole production system, it seems reasonable to postulate that high variance of component populations is likely to be associated with increased probability of system transformation to a new community niche. Thus, where population variance depends importantly on innate characteristics of particular stocks, the associated risks of stock management intervention involve not only the population, but also the community of which it is a part.

Accordingly, it appears that questions of the stability of entire production systems cannot be approached piecemeal on a stock by stock basis, overlooking the nature of their interactions. On the other hand, it is not sufficient to examine system dynamics solely at the aggregate population level, as some portion of the aggregate population variance may be a consequence of the scale of population definition. A "top-down" approach is therefore indicated, wherein the system behaviors are first explored (external analysis), followed by internal analysis to reveal the underlying processes (Kerr 1974a, 1976; Silvert 1981; Dickie and Kerr 1981). In effect, successful system analysis must bridge two or more levels of ecological organization.

The question of providing appropriate system descriptions at the community level of ecological organization has not been as well explored as have the conventional forms of internal analysis. Nevertheless, several useful approaches exist, one of which will be emphasized in what follows.

In seeking conservative behaviors at the community level of organization, it is useful to consider scale factors that may be involved. The effects of perturbation can potentially be expressed over a variety of time scales, ranging from the relative immediacy of behavioral compensation through the lengthier scales of physiological, demographic, and ecological response, and ultimately to the evolutionary scale. In turn, genetic change, on the evolutionary scale, may be incorporated through modifications expressed primarily on any of the shorter scales. The latitude for phenotypic response on all scales is set by genetic limits, but for many types of biological response the latitude is typically broad. The potential niche is ordinarily much larger than the realized niche for a given habitat, although less so for depauperate faunas. In practical terms, it is of considerable value to the fisheries manager to understand the available response latitudes and associated time scales that are characteristic of the resource system being managed. For example, how long would it take for the Great Lakes fish communities to return to their virgin state if there was no fishery, all environmental impacts were removed, and introduced species were exterminated?

There is no single, absolute time scale that can be applied to a biological production system. Physiological time for a lake trout (*Salvelinus namaycush*) may correspond in absolute

terms to a demographic or even evolutionary time scale for the cladoceran on which it feeds. To be comparable, response times must be expressed in terms of generation time, which is itself a complex function of variables such as organism size. Expressing response times in terms of generation time suggests that the size structure of a production system offers a compact means for description of the system response to a stock perturbation.

There is evidence to suggest that ecological production systems exhibit characteristic size spectra. This has been shown for a variety of marine pelagic (Sheldon et al. 1972), marine benthic (Schwinghamer 1981), and freshwater (Sprules 1981) communities. A complete theory for the generation of characteristic Sheldon spectra does not yet exist, although the phenomenon is understood in outline. Essentially, the size spectrum results primarily from the disparities of predator and prey body sizes interacting with the size-dependent variation of turnover rate (Kerr 1974b). Where physical substrate is utilized, as with the benthic communities studied by Schwinghamer (1981), the substrate effect further modifies the shape of the spectrum. Given the nature of its generating mechanism, it follows that the size spectrum is amenable to transient or permanent deformation, in consequence of a variety of types of perturbation (Kerr and Vass 1973; Silvert and Platt 1978). Accordingly, observation of the system size spectrum offers a means for evaluating response of entire systems to perturbations such as stock modification.

The foregoing picture is predicated on ecological process, and does not include consideration of the typological composition or the functional roles of the various stocks and species which make up the production system, except as is approximated in terms of their size dependence. In that sense, the size spectrum is an integral descriptor of community structure, which is itself a reflection of the community niche. Within that general structure, the individual stocks of each species are embedded, and their specific roles assessed in terms of their realized niches.

There is thus ample reason to suppose that management of fish stocks cannot be undertaken in isolation from the whole fish production system. Various system conservatisms, such as the Sheldon size spectrum discussed above, serve as strong constraints on the structural organization of systems. Within such constraints, the functional roles of size fractions of the system appear relatively invariant, although subject to deformation by perturbations that themselves may appear small, e.g. stock introduction. In turn, the dynamics of individual populations in the system may be highly sensitive to stock manipulations. Bearing the foregoing concepts in mind, we now focus on some problems of concern to fisheries managers.

Problems

The principal problems facing fisheries managers in the Great Lakes concern changes in fish stocks over time through the agencies of exploitation, eutrophication or other classes of environmental degradation, and invasion or introduction of exotic species (Loftus and Regier 1972). Each of these effects has been thought to change the genetic structure of stocks in the Great Lakes (e.g. Smith 1964) and, consequently, alter the realized niches of species. The recognized consequence is embodied in reverberations of community niche boundaries through changes in individual species boundaries or through intrusion of new species niches into the community niche complex. The ultimate effect includes losses of preferred fish species, usually from the top trophic levels, species that integrate and therefore are critical in the maintenance of community harmony. Although total fishery yield tends, within limits, to be maintained in the face of such stress (Regier and Hartman 1973; Sutcliffe et al. 1977), economic benefits may decrease because of the loss of larger, quality species (Regier 1973). The chief characteristic of the perturbed biotic community becomes its wide variance about, or departure from, a harmonic steady-state and the lack of predictability of community metabolism or behavior. Symptoms may range from the total spectrum of extreme density-dependent effects (increased growth and decreased age to maturity are two examples) to other more lasting effects such as reduced mean size, complete eradication of stocks or species, introgressive extinction of genetic or phenotypic stocks, unpredictability of proportionate stock composition within the community, pathogenic eradication of species, or simply general instability of the system.

Environmental Degradation

Eutrophication, toxic wastes, sedimentation, and physical alteration of the environment may have dire effects on genetic stock composition in lake systems. Depending on spatial distribution of the stress, and its temporal duration, fish communities may be altered almost imperceptibly or with unrelenting selection against the survival of certain species or stocks (Loftus and Regier 1972). This selection operates intensively at the most vulnerable links of the metabolic and behavioral chain, that is, at the reproductive and early life history stages of fishes. In the former instance, the adults of many fish stocks form aggregations in shallow inshore waters or streams where they may be particularly susceptible to cultural stresses emanating from the land. Spawn deposited on the shallow substrate may suffer similar effects, whereas the early life history stages of fishes are vulnerable because of a total dependence on an appropriately structured food web (Ware 1977).

Losses of specific spawning stocks that were probably unique genetically have been widely documented in the Great Lakes region (Loftus and Regier 1972). Stream-spawning stocks were especially vulnerable to the earliest perturbations, which included the installation of gristmills on the spawning streams of the Atlantic salmon (*Salmo salar*) (Smith 1972), and deforestation of the watersheds of Lake Ontario (Huntsman 1944). Other examples of loss of spawning stocks through environmental degradation include early losses of river-run and lake stocks of various species due to deforestation, mining, industrial effluents, or high sedimentation rates on spawning grounds, arising from land erosion or as a secondary effect of eutrophication in contiguous lakes (Langlois 1954). The latter effect is particularly selective against lake trout stocks and may be one of the factors restricting natural reproduction of offshore stocks in Lake Michigan.

Drastic changes in mean ambient water temperatures, or the influence of warmwater discharges from a variety of sources,

may operate selectively against native fish stocks and at the same time favor the invasion of exotic species. Hence the sea lamprey (*Petromyzon marinus*) may have been provided with some slight reproductive advantage in the upper Great Lakes following large-scale watershed deforestation (Lawrie and Rahrer 1972), whereas alewives (*Alosa pseudoharengus*) may have gained a similar advantage when warmwater effluents caused marked increases in inshore temperatures. Periodic massive die-offs of the latter species (Colby 1971) suggest that they persist in this highly variable environment through the rapid and opportunistic flooding of available habitat with waves of progeny. Whether this survival strategy could be successful in a more stable environment in competition with native stocks which had evolved there is problematic.

Exploitation

The ultimate effect of exploitation on fish communities is often markedly similar to that of environmental degradation, that is, a diminution of niche variability as expressed through selection against particularly vulnerable genetic or phenotypic stocks. This effect comes about through the reordering of niche boundaries following the partial or complete removal of a particular stock or substock, or the genetic displacement of specific (and important) stock characteristics to insignificant levels.

This selective effect of exploitation on fish stocks has been demonstrated by Ricker (1981) for the five species of Pacific salmons (*Oncorhynchus* spp.). Selection was due to the physical nature of the gear and applied specifically to trolls and gill nets, as opposed to seine fisheries which were nonselective or, at most, only weakly selective. The overall effect of gear selectivity has produced a cumulative genetic change in individual stocks. Gear selection for large individuals of some species (Regier and Hartman 1973), or particularly vulnerable spawning runs, especially of adfluvial spawners, has been demonstrated in Great Lakes fisheries (Loftus 1958), and the genetic consequences are undoubtedly similar to those experienced with the Pacific salmon stocks (Calaprice 1969; Ricker 1981). Indeed, niche alteration through exploitation of specific stocks on the Great Lakes may be of even greater significance because of the intricate connectivity of the various components of the fish community there.

Exotic Species

The relationship of genetic composition of stocks to niche dimension, and ecosystem structure and function, is apparent when examining the effects of introduced stocks on an existing community. The invasions of new species into the Great Lakes through canals or diversions, or through deliberate introductions, have created stresses on native stocks not dissimilar to those of environmental degradation and exploitation. However, whereas the latter two stresses have disrupted community harmony of natural stocks through the removal of key components essential to maintain low levels of variance in niche interactions, introduction of new species has resulted in massive intrusions into community niche space. These intrusions create reverberations throughout the biotic community, resulting in a reordering of genetic material and the associated phenotypic responses, until a new steady-state is achieved. In some instances, this new steady-state may require a time scale of evolutionary magnitude because of the short-term, opportunistic responses of exotic species such as the alewife and rainbow smelt (*Osmerus mordax*), which on a periodic basis create oscillations throughout the system by use of their particular strategy of survival.

If we accept the thesis of MacArthur and Wilson (1967) that all organisms fall along a cline of colonization strategies, then the predominant stocks indigenous to the Upper Great Lakes and Lake Ontario were rather more *K*-selected than *r*-selected. *K*-selected species exhibiting low fecundity and slower growth rates would tend to prosper in austere oligotrophic environments with relatively predictable hydrologic regimes, and low food abundance. In the upper Great Lakes and Lake Ontario, the lake trout was a major top predator that formerly maintained the steady-state of prey stocks, principally the ciscoes and whitefishes (*Coregonus* spp.) and the deep-water sculpin (*Myoxocephalus quadricornus*). The lake trout exhibited one extreme of *K*-selection in fish species, while the coregonines and deep-water sculpin showed greater *K*-selection characteristics than did the recently invading species, especially the rainbow smelt and the alewife, both of which are clearly *r*-selected species.

Consequently, nature's solution to the unique problem of glaciation and deglaciation effects has been to create species with rapid phenotypic response to environmental heterogeneity, while still retaining the long-term advantage of *K*-selection. The observations of Dehring et al. (1981) on lake trout stocks and Todd (1981) on the phenotypic variability of the ciscoes would tend to support this hypothesis. The *r*-selected species, on the other hand, use the tactic of genetic swamping to gain advantage opportunistically over native species in the face of rapid and anomalous environmental changes due to man's activities.

Dominant taxa of the upper Great Lakes and Lake Ontario in pristine times exhibited a phenotypic plasticity, a definite advantage in the exploitation of scarce biotic resources in large, austere, and spatially diverse oligotrophic systems. This rapid phenotypic adaptability exhibited by the lake trout and ciscoes has a parallel in the genotypic variability of the endemic cichlids of the Great Lakes of Africa, especially Malawi and Tanganyika. In the latter instances, genetic polymorphism has been described (Fryer and Iles 1972); possibly this occurrence is due to the geological time scale of coevolution rather than through the exigency of short-term phenotypic plasticity of stocks, as exhibited in Scandinavia (Svärdson 1965), the Great Lakes (Koelz 1929), and other austere environments. Where the creation of a new environment occurs, as in the period subsequent to glacial recession, then optimization of niche space occurs through phenotypic diversification, as with the Lake Superior lake trouts and ciscoes. This phenomenon has been observed in the upper Great Lakes to arise not only from the existence of environmentally diverse habitats separated by effective ecological barriers, but may be due particularly to the isolating effect of intense predation in the segregation of highly plastic stocks of fishes. Hence the lake trout and burbot (*Lota lota*), two efficient piscivores, may have been instrumental in the creation of sympatric phenotypic stocks of ciscoes in the upper Great Lakes by confining them to pockets of predation refugia. Following the highly selective predation of the sea

lamprey on these two effective predators, rapid introgression in the ciscoes was suggested as a possible cause of the marked decrease in their phenotypic variability (Smith 1964). In general, a decrease in polymorphic variability of a taxocene (Chodorowski 1959), whether genetically or environmentally caused, will reduce its efficiency in exploitation of the environment through the reduction of ecological opportunities (Dobzhansky 1951).

Community Effects of Stressors

Apart from direct impact upon the fish communities themselves, fish stock perturbations affect other parts of the production system. As Holling (1978) has pointed out, the spatial distribution of stress effects is not simply a monotonic decay centered about the point of stress, but in fact is often spatially heterogeneous within the system. Thus, for example, an exploitation stress on a pelagic fish community may cause marked changes in a spatially discrete benthic community. Although much remains to be learned about the pathways that mediate perturbation transfer within and among aquatic communities, there is sufficient information to identify some of the key linkages among major system components. We trace these here, in terms of effects on community size composition.

It is important to recognize that size changes are ultimately a result of shifts in gene selection and relative fitness in the stocks comprising the system. If the stressor directly or indirectly modifies realized niche, then a change in relative fitness of individual gene complements will result, with attendant pressure for change in genetic constitution elsewhere within the system. The degree of genetic variability within the component stocks, and the amount of realized niche compression induced among them, among other factors, will determine the form of structural change within the community.

For the zooplankton, fish predation has been shown to have major effects on zooplankton species diversity, abundance, production, and consequently, size composition (Hrbáček et al. 1961; Brooks and Dodson 1965; Galbraith 1967; Kerfoot 1980). Because of these substantial effects, fish are often considered to play roles that are critical in the form of community structure. In the absence of fish predation, it is usually found that large zooplankters tend to dominate the animal plankton (Hrbáček and Hrbáčkova-Esslová 1960; Lötmarker 1964; Brooks and Dodson 1965; Galbraith 1967). One possible explanation is the hypothesis that larger species filter more water per unit time, thus acquiring more net or surplus energy than smaller species (Brooks and Dodson 1965). In the absence of selective predation on the larger forms, increased surplus energy translates to greater egg production and a buildup of larger forms in the zooplankton. Another hypothesis is that small zooplankters are controlled by predation of larger invertebrates (*Chaoborus*, *Leptodora*, *Asplanchna*, etc.) and do not achieve numerical dominance because of the high predation rate (Hall 1964; Dodson 1974). The latter view is supported by changes in zooplankton structure following the introduction of large exotic zooplankters, as was shown in Lake Tahoe with *Mysis relicta* (Goldman 1981). The two hypotheses are not mutually exclusive, and it seems likely that both processes are important at times.

Accordingly, fish predation has an opposite effect to that of invertebrate predation in determining the size structure of the zooplankton. With invertebrate predation, zooplankton species sizes tend toward large particles. Fish, on the other hand, prey selectively on the larger zooplankton species. If their predation rate is high enough, and the size spectra of individuals consumed include all adults, then the large species will be reduced, releasing the smaller species from competition with the larger forms. In turn, dominance of small zooplankton affects fish growth and survival in future generations and, as will be discussed below, the particle size distribution of the primary producers. But, although the foregoing processes seem relatively well supported, the existence of apparent exceptions among Arctic zooplankton communities (O'Brien et al. 1979) suggests that our understanding of the factors determining zooplankton size composition is by no means complete.

The size composition of phytoplankton is controlled internally as an optimal response to the light, nutrient, and thermal regime (Shuter 1979), and externally by grazing (Burns 1968, 1969; Porter 1973; McNaught et al. 1980). Grazing effects may be either direct, as with zooplankton grazers and some planktivorous fishes, or indirect, as with the effects discussed above of planktivorous fishes on the size structure of the zooplankton.

Little is known of the direct effects of fish grazing on phytoplankton size composition. Fryer and Iles (1972) reported that chlorophyll levels were reduced 95–99% after a swarm of filter-feeding cichlids strained an area in one of the African Great Lakes. Although the direct consequences of fish grazing on phytoplankton size structure are not known, size selectivity would cause the same kinds of displacements as have been observed for zooplankton grazing on phytoplankton (Steele and Frost 1977).

Where large zooplankters are present, they are able to feed on both large and small phytoplankton particles (Porter 1977; Steele and Frost 1977). Because of the differential production rates of large and small particles, small forms would dominate in these circumstances. If larger zooplankton are reduced by size-selective fish grazing, however, then the remaining small zooplankton forms would be unable to graze the larger phytoplankton and the latter would dominate the phytoplankton. Spencer (1981) has shown that such size displacements affect water chemistry parameters, periphyton, phytoplankton, and macrophyte production, indicating further implications for the ramifying effects of perturbations throughout a production system.

Water quality, in turn, affects phytoplankton species succession (Lund 1964; Hutchinson 1967) and particle size distribution. Blue-green algae (generally large particles) are competitively superior to other phytoplankton particles at low carbon dioxide levels (King 1970, 1972; Shapiro 1973), low light levels (Walsby 1977; Spencer 1981), high temperature (Fogg 1965), and in nitrogen-poor water (Horne et al. 1972). Gelatinous green algae also are dominant under low nutrient conditions, because they pass through zooplankton alimentary canals alive, collecting from digested green algae vital growth nutrients (PO_4, N), which are used for growth when returned to the water mass (Porter 1977). The buildup of large inedible (blue-green algae) or indigestible (gelatinous green algae) particles results in a shift to smaller zooplankton (Porter 1977; Taylor and Gerking 1980),

which are unaffected by large phytoplankton species abundance because they feed on smaller phytoplankton species, and on bacteria, which are numerous during phytoplankton blooms (Haney 1973). Decreases in the large zooplankton species, in turn, directly affect planktivorous fish growth (Galbraith 1975).

The size composition of the benthos is presumably affected by similar, size-dependent, grazing effects, but these have not been well studied. In all cases examined, fish predation has reduced the biomass (B) of the benthos and increased its production (P) (Ball and Hayne 1952; Gerking 1962; Hall et al. 1970). Increased turnover rates (P/B) are usually associated with the release of density-dependent controls and ultimately with shifts to smaller mean size of the assemblage. Interestingly, Banse and Mosher (1980) point to anomalously low turnover rates for the temperate meiofauna in general, and posit that, in this instance, small size may provide a refuge from predation. If so, there may be differences in the regulatory processes reflected in benthic size composition. Certainly, there is an important substrate effect that is lacking in the pelagic zone.

Physical substrate introduces heterogeneity in itself, and provides the potential for structural elaboration, complicating prey–predator relations. Schwinghamer (1981) has determined that the characteristic size spectra of benthic organisms are strongly affected by the availability of substrate. But, although some important differences appear to exist, it again seems clear that perturbation effects elsewhere in the community can be expected to affect benthic size composition. Accordingly, there is reason to expect general patterns of perturbation effect to be expressed by size displacements throughout aquatic communities.

Some Options

In consideration of the major problems of environmental deterioration, introduction, invasion of exotics, and overexploitation (Loftus and Regier 1972), a concerted management effort is necessary if the biotic resources of the Great Lakes are to continue to be of value to man. Many options are available to environmental managers, including the following.

Type 1. Allow the aquatic ecosystem, including the component biota, to ebb and surge according to the cultural stresses imposed on it, i.e. take no constructive action.

Type 2. Impose more rigorous regulatory controls to prevent overexploitation of fish stocks and other aquatic resources.

Type 3. Impose tighter controls on effluent wastes, watershed development, and other environmental perturbations, and introduce environmental mitigation and rehabilitation procedures.

Type 4. Reconstitute a fish community that would be capable of optimizing the resources of the environment for long-term maximum output, that is, predictable yield.

Type 5. A combination of types 2, 3, and 4 above.

If the ultimate goal for Great Lakes fisheries management is for optimum use of the total resource, including recreation, food, and esthetic values, then the objective for restoration should include considerations concerning the type of ecological community mix that will provide the greatest satisfaction for all potential users. On this basis, the type 1 approach, where no significant intervention is taken to protect or improve the environment or the fishery, can only result in ecological disaster, assuming a continuing rate of cultural impact in the Great Lakes watershed. Although many fish will persist as the several stresses increase in magnitude, certain vital links will disappear, such as top predators, salmonids, and sensitive food organisms such as *Mysis* or *Hexagenia*. These organisms may be critical components of a harmonic biotic community and their losses may set the system into erratic oscillation, creating innumerable social difficulties including the following: (1) massive fish die-offs requiring costly cleanup, (2) loss of revenues from commercial and sports fisheries through high toxic levels in the catch, (3) increased expenditure in capturing fishes of smaller mean size remote from shore, and (4) generally lower commercial value of the surviving selected species. The consequences of the "do nothing" approach will be increasingly evident with time and ultimately may be socially unacceptable to the citizens of the Great Lakes megalopolis.

A type 2 approach that imposes tighter regulation on fishery exploitation may alleviate adverse selection against predator species or large individuals and thereby retain a semblance of steady-state in the total fish community. Methods have been widely published for optimizing the potential output of a particular fish population (e.g. Larkin 1977) to derive greatest social or economic benefits, but only rarely have these proposals considered the genetic uniqueness of the stocks and their preconditioning to a specific environment. Therefore, although regulatory measures for the optimization of a fishery may prove to be a biological palliative of temporary nature, as often as not they serve to alleviate only a portion of the problem.

The type 3 approach, which corrects or alleviates environmental degradation, ideally would terminate in aquatic system rehabilitation. Environmental stresses may be extremely selective against certain stocks or species. River-run and nearshore stocks appear to be particularly susceptible because of their proximity to polluting sources, shore development, and other unstable processes operating on or near the littoral. Although many species may be temporarily exempt from these effects because of their pelagic life style, those that are required to reproduce on clean boulder shoals in the shallow waters of streams, or on the nearby littoral, may lack adequate annual recruitment because of their proximity to toxic, organic, or thermal effluents. Environmental mitigation and rehabilitation, therefore, may be the best single measure to ensure adequate reproduction of various fish species, including most nearshore predators.

The reconstitution of a disaggregated fish community (type 4 approach) into a harmonic community of predictable and steady yield variance, in which each component stock or species is harvested proportionately to its internal turnover rate, would at first glance appear to be an ecologically sound and admirable position for a fishery manager to take. Unfortunately, there are some flaws in this simplistic formula, not the least of which concerns the necessity to consider the three SCOL stresses (Loftus and Regier 1972) of environmental degradation, overexploitation, and the intrusion of new species into the community mix. Consequently, a consideration of community reconstitution, without regard for the

conditions that disaggregated the community in the first place, would constitute a myopic approach to the problem. Moreover, as the stresses continue, change, or become more severe, there is need to revise the mix. The rational solution is to reduce or alleviate the stresses as far as possible before attempting community reconstitution.

An alternative approach that has gained favor in some quarters is to develop fish stocks that may be inherently (genetically) resistant to the various stresses, especially those that are environmentally induced. An obvious deficiency in this tactic concerns the loss of the "miner's canary" function of our native organisms. A close analogue to the development and culture of fish stocks with specific resistance to environmental toxicants of cultural origin might be the genetic selection of a Welsh coal miner's canary that could live in conditions that would kill miners (H. Harvey, Univ. Toronto, personal communication). Any genetic engineering would be put to better use to develop stocks suitable for a rehabilitated environment approximating conditions on the Great Lakes about 100 yr ago (Francis et al. 1979).

Re-examination of our previously established target for Great Lakes fisheries management is appropriate here. This objective is the assembling of stocks (harmonic community) that are mutually adjusted to maximize their aggregate genetic potential for exploiting the resources of the environment that they occupy. Many options come to mind, of which three are expanded below.

1) Strive for maximum total biomass at high turnover or production rates. Implicitly, this scenario conjures up the picture of a monoculture of fishes feeding at the primary trophic level, with little energy loss attributable to trophic transfer. Social considerations are important in this scenario and its establishment assumes a need for low-valved protein, a condition not currently extant in the Great Lakes region. Aside from this obvious shortcoming it is not likely that this scenario would work as might at first be imagined. The implicit understanding that monocultures of fishes feeding at lower trophic levels have greater ecological efficiency resulting in larger productivities is a common misconception (Kerr and Martin 1970). Although this concept may apply to small, shallow lakes or ponds where environmental heterogeneity is low, in large bodies of water on the order of magnitude of the Great Lakes, niche packing is essential for the extraction of environmental resources with maximum efficiency.

Another important consideration pertains to the bioeconomics of harvesting small particles (e.g. rainbow smelt, alewives) over wide geographic distances, considering the energy expenditure necessary to effect the harvest. Although monocultures of low-valued protein may support profitable fisheries during periods of high concentration, far greater profitability would likely accrue from a mix of more valuable species feeding advantageously at different trophic levels.

Additionally, monocultures are especially vulnerable to epizootic pathogens, and complete eradication is more likely to occur than in the case of mixed stocks. All things considered, monocultures are probably best restricted to intensive cultural and propagation practices in small, shallow bodies of water, or perhaps for cage culture in the littoral zone of the Great Lakes. Large-scale cage culture is undoubtedly a prospect of undetermined practicability for the future (Bardach et al. 1972).

2) A second option for maximizing fish yield consists of the reconstruction of a "balanced" fish community utilizing fish species to fill the appropriate trophic levels and size ratios appropriate to predator–prey considerations. The ultimate effect becomes planned niche packing, insofar as niche dimensions of the various species may be known. At present, this reconstitution of disaggregated fish communities is usually attempted with nonnative fish stocks, which may have particular phenotypic attributes seemingly appropriate for the apparent community hiatuses. Through such a line of reasoning, coho (*O. kisutch*) and chinook (*O. tshawytscha*) salmon were introduced into the Great Lakes to utilize the abundant forage in the form of rainbow smelt and alewives. These salmon grow more rapidly than native predators and, in the case of the chinook, grow to a larger mean asymptotic size than the native lake trout. They are fondly regarded by sportsmen and have the potential for supporting a viable commercial fishery.

There are some drawbacks to these procedures that should be considered carefully, prior to any large-scale introduction of nonnative species. For the two Pacific salmons, toxicant loads in some instances have accumulated in the fatty tissues at concentrations higher, on average, than those found in native top predators. This may result from the narrower range of food items consumed by the salmon. Their preferred food consists of fishes which are themselves bioaccumulators occupying, for the most part, secondary and tertiary trophic levels. The native lake trout, on the other hand, feeds over a broader range of food organisms (Stewart et al. 1981) and consequently has less potential for toxic material accumulation.

Introduced exotics in the Great Lakes have traditionally been species that were amenable to hatchery culture, and may have been inadvertently selected for phenotypic characteristics that offer them little survival potential at the weakest link in their life history, the reproductive and early feeding stages. The ultimately large size attained by the coho and chinook salmon in the Great Lakes may be a temporary phenomenon relating to a superabundant food supply. This size characteristic would lack survival advantage if future food abundance declined or if mean particle diameters of food portions were reduced significantly. Preliminary examination of mean size data for the pink salmon (*O. gorbuscha*) in Lake Superior after 13 generations showed a noticeable reduction in mean length. Any short-term cultural advantage gained from the introduction of Pacific salmon in the Great Lakes, resulting in immediate high yields, may be overridden in the long term by continuing low levels of mean yield. Each new exotic introduction resulting in reproducing fish stocks may reduce the chance of achieving the long-term stability of a harmonic community. Although there may be hope for successful community structuring in the future through genetic engineering, the current state of the science suggests that present techniques may inevitably be associated with unexpected and possibly dire ecological consequences.

The economic benefits of exotic introductions, which have not yet been adequately assessed, may also prove disappointing over the long run. The creation of a need for a resource where no need existed previously can result in economic ramifications of unpredictable magnitude. A simple

benefit–cost assessment of continuous salmon planting without the establishment of reproducing stocks may appear to be profitable until a closer look is taken at the quantity of new money generated by the operation. The more normal situation created by the establishment of a new fishery is an opportunistic diversion of funds from a pre-existing recreation or industry to support the establishment and growth of the new fishery. Because of the tenuous nature of reconstituted fisheries and the ecological uncertainties concerning them, economic profitability becomes a game of chance. A future scenario of decaying marinas, replete with decrepit troll boats and lakeshore ghost towns, is not beyond the realm of possibility.

3) This option entails the continued management of the natural community but with full recognition that the "pristine" condition may not be attained. The knowledge that a diverse community of fishes withstood a commercial fishery of increasing intensity for the first 50 yr of exploitation on the Great Lakes and yet retained a constancy of yield is an ecological fact of great significance (Ryder 1965; Regier and Hartman 1973). The resilience of the fishery was sustained by system integration, in the form of niche interactions and community feedbacks. This condition led to the impression that fish communities in stable environments were incapable of being fished to extinction, a position often stated by the late A. G. Huntsman. This philosophy soon failed when fish communities had additions to their exploitive stress load, namely environmental degradation and invasions of exotic species, especially the sea lamprey. It has already been shown that these three unrelated stresses were not compensatory, but tended to be additive, eliciting the same ecological response from relatively stable communities. All three stresses tended to focus on the larger brood stocks, particularly when they were concentrated in spawning aggregations, or alternatively at the vulnerable egg or early life history stages. The key, then, to the maintenance of an ensemble of stocks that are mutually adjusted to maximize their aggregate genetic potential for exploitation of the environmental resources would seem to be through the process of natural reproduction. Maintenance of this condition requires concerted attacks on all three fronts, namely, exploitation, environmental rehabilitation, and control over introductions.

The long-term economic advantage that accrues through the maintenance of natural communities of wide genotypic variability is self-evident. Fish harvests of predictable quantities and proportionate species composition allow commercial fishermen to plan their fishing strategies and retain the appropriate gear for maximum efficiency of harvest. Allocation equitability becomes accordingly simple because wide short-term fluctuations in stocks do not require constant quota adjustments. Government control and intervention through regulation or stocking becomes minimal and management costs are reduced. Processing and marketing capitalization is similarly optimized. Social benefits are also realized, as resource users reap a harvest of fish species to which they are accustomed and for which traditional esthetic values or modes of preparation are well understood and appreciated.

Conclusion

Current ecological theory suggests that genotypic characteristics form the basis for potential or fundamental niches of populations or stocks. The scope of each biotic and abiotic niche dimension, therefore, is genetically determined but is further constrained by exogenous environmental effects into a realized niche or an operational niche. Aggregations of realized niches of co-evolving species or stocks constitute a harmonic community niche, which may be sensitive to external intrusion through the introduction of nonnative species. Heavy exploitation and environmental degradation further constrain community niche dimensions until the community niche system loses its resiliency and integration, breaking down into a disaggregated ensemble of opportunistic stocks. System stability is lost and system output in terms of fisheries yield becomes unpredictable, both qualitatively and quantitatively.

The ecological reverberations ensuing from poor management practises extend into socioeconomic systems and are disruptive of both life styles and currency flows. Recreations and industries most closely dependent on the need for continuing aquatic resource production are first affected. Once their normal operations become disrupted, however, the tidal wave of instability floods secondary and tertiary interests, with little or no negative feedback that might tend to stabilize the total system complex.

Fisheries managers on the Laurentian Great Lakes are in a position to stem the initial buildup of this flood tide through constructive application of current ecological theory, which dictates a support for, and rehabilitation of, co-evolving native stocks.

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Glossary

Niche	The abstract hyperspace generated by assigning a metric to each environmental parameter affecting an organism's metabolic scope for activity
Potential niche	The niche hyperspace an organism is genetically equipped to occupy in the absence of environmental constraints
Realized niche	The niche hyperspace actually occupied by an organism in a given ecosystem
Community niche	The composite niche hyperspace realized by all component organisms in a community, resulting from their mutual interactions
Niche packing	The dynamical process that leads to the formation of a harmonic community
Harmonic community	A steady-state community in which the component biota have a high degree of integration in their niche interactions due to co-evolution
Astatic community	A weakly integrated aggregation of biota, highly variable in time, usually because of cultural stress, especially the introduction of, or invasion by, exotic species

Guidelines for the Culture of Fish Stocks for Resource Management[1]

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Examples of desired genetic changes produced in fish by selective breeding are contrasted with those of unintentional and often harmful genetic changes resulting from artificial propagation over prolonged periods, e.g. reduced longevity and reduced temperature tolerance. Evidence for undesired effects caused by the hatchery environment on captive fish stocks is also presented, e.g. precocity, inappropriate feeding behavior, and the risks posed by artificial rearing techniques are discussed. Methods for identifying both genetic and environmentally induced changes are outlined along with experimental designs for distinguishing between them. Some practical recommendations are offered for establishing, developing, and maintaining brood stocks in hatcheries and for managing wild fish populations in ways that maximize genetic variability while avoiding the occurrence of undesirable changes. Adherence to the recommended procedures will improve progress in fisheries rehabilitation efforts.

Key words: fish culture, genetics, environmental effects, brood stocks, resource management

HYNES, J. D., E. H. BROWN JR., J. H. HELLE, N. RYMAN, AND D. A. WEBSTER. 1981. Guidelines for the culture of fish stocks for resource management. Can. J. Fish. Aquat. Sci. 38: 1867 – 1876.

Nous examinons dans l'article qui suit l'effet potentiellement nuisible des techniques d'élevage des poissons sur des stocks destinés à la gestion des pêches et l'échec concommittant à atteindre les objectifs désirés. Nous donnons des exemples de changements génétiques souhaités résultant de croisements sélectifs de poissons, par opposition à des changements génétiques accidentels et souvent nuisibles découlant d'une propagation artificielle pendant de longues périodes, par exemple consanguinité, longévité réduite et tolérance moindre à la température. Nous décrivons également des cas d'effets non désirés résultant de certains aspects de l'environnement de l'écloserie sur les stocks de poissons captifs, par exemple précocité et comportement alimentaire inapproprié, et nous analysons les risques que comportent les techniques d'élevage artificiel. Nous décrivons brièvement des méthodes d'identification de changements tant génétiques que provoqués par l'environnement, ainsi que des protocoles d'expériences permettant de les distinguer. Viennent ensuite quelques recommandations pratiques pour l'établissement, le développement et le

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maintien de stocks reproducteurs dans les établissements de pisciculture et pour la gestion de populations de poissons sauvages de manière à porter au maximum la variabilité génétique, tout en évitant des changements indésirables. En conclusion, l'application des méthodes décrites améliorera les chances de succès de la réhabilitation des pêches.

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WIDE variations in the success of using hatchery-reared fish to enhance, rehabilitate, and develop fish stocks in the Great Lakes have caused much concern over possible genetic and environmentally induced changes in the hatchery product. These changes, which are often called "domestication effects," can adversely affect the development, morphology, physiology, reproduction, and survival of the fish propagated for stocking; ultimately the survival of native fish populations may be affected. Fisheries managers must therefore design breeding, rearing, and stocking programs in ways that minimize the harmful side effects of hatchery propagation. Domestic and wild brood stocks must be developed and utilized with due consideration given to maintaining the genetic integrity and maximum genetic diversity of stocks being managed. Progeny obtained directly from wild brood stocks must also be reared by procedures and techniques that preserve the basic gene pool of the donor stock.

The purpose of this paper is therefore threefold: (1) to review evidence in the literature of both genetic and environmentally induced changes in captive fish stocks; (2) to identify briefly methods for detecting genetic changes in, and environmental effects on, captive stocks, as well as methods for distinguishing between them; (3) to outline recommendations for the maintenance of the genetic character, in particular the genetic variability, of cultured fish stocks, and means of detecting and avoiding the potentially detrimental side effects of the hatchery environment.

In the discussion that follows, captive stocks are understood to include all stocks reared under artificial or controlled conditions in fish culture facilities for all or any portions of their life cycles. This includes brood stocks maintained within fish culture stations, wild or native stocks from which eggs are collected and fertilized in the field, and progeny of the latter raised to fingerling or later stages of development in the hatchery. The definition of stock proposed by Ricker (1972) is also adopted here, i.e. "the fish spawning in a particular lake or stream (or portion of it) at a particular season, which fish to a substantial degree do not interbreed with any group spawning in a different place, or in the same place at a different season."

Evidence for Genetic Changes in Captive Fish Stocks

Genetic changes in captive fish stocks fall into two broad categories: (1) intended changes from selective breeding for specific traits, and (2) unintended changes related mainly to inbreeding. Both types of genetic change may have serious consequences on fitness and survival in the wild because of the reduction in genetic variability. The unintended category of genetic change is the most important wherever fish culture is used as a tool in the management of Great Lakes fish stocks, because of their long life cycles and the many years that such programs must be maintained. Indeed it has often been necessary to hold certain strains of Great Lakes fishes in the hatchery environment for several generations. The unintended adverse genetic effects of these practices are not well documented in the literature, although a few examples of unintended genetic changes have been observed in captive stocks as indicated below.

SELECTIVE BREEDING

Many physical and developmental attributes of fishes have been the object of selective breeding studies. Donaldson and Olson (1956), for example, selectively bred for faster growth in the rainbow trout (*Salmo gairdneri*), and Gall and Gross (1978) further demonstrated the genetic basis for control of growth rate in that species. In addition, Donaldson (1970) reported increased egg production and earlier maturity from selective breeding in rainbow trout. Similar carefully controlled breeding studies on carp (*Cyprinus carpio*) in Israel (Wohlfarth and Moav 1972; Moav 1979) have provided some gains in growth relative to use in aquaculture. Distinctive morphological changes including reduced numbers of scales and bones have also been effected in the common carp in Europe by selective breeding in historical times to provide a better product for the table. Recent studies in Israel (Moav 1979), however, demonstrated the occurrence of only small variations among different strains of carp, suggesting a low heritability for intramuscular bones. In tropical aquarium fishes, numerous physical features, including body form, fin shape, and color, have been selectively modified for ornamentation (Gordon 1957).

Various physiological characteristics as well have been shown to be stock specific. Swartz et al. (1978) demonstrated strain differences in survival ability of brook trout (*Salvelinus fontinalis*) exposed to low pH and Gjedrem (1976a) showed that tolerance to low pH values differed among genetically distinct strains of brown trout (*Salmo trutta*) in Norway. Both examples indicate the possibilities of developing acid-tolerant strains of those species for planting in waters with decreasing pH values caused by acidic precipitation. Studies with the splake (*Salvelinus fontinalis* × *S. namaycush*) have demonstrated clearly that retention of swim bladder gas and the consequent ability to occupy deep water can be selected for in species hybrids (Tait 1970; Ihssen and Tait 1974). In other studies with splake, Ihssen (1973) demonstrated the heritability of resistance to lethally high temperatures. Donaldson and Olson (1956) also claimed increased tolerance to warm temperatures in rainbow trout following several generations of selective breeding, although their studies lacked control groups.

Wolf (1953) was among the first to discuss the possibility of selecting for disease resistance in fishes. He cited examples of mortality in brown trout and brook trout from ulcer disease

and furunculosis, which indicated differences in resistance to those diseases among different strains. Gordon (1954) showed the genetic basis for resistance to the development of thyroid tumors in hybrids of the platyfish and swordtail (*Xiphophorus* spp.) in aquaria. Increased resistance to unspecified diseases through selection was also reported for rainbow trout (Donaldson and Olson 1956). A program designed to select for furunculosis-resistant brook trout stock was reported by Ehlinger (1964), and Wolf et al. (1968) described methods for the selection of a brood stock free of IPN virus in the same species. Resistance to dropsy in the common carp was improved through selective breeding in Russia (Kirpichnikov et al. 1979).

In the examples cited above, the intention of selective breeding has been to increase the incidence of one or more desired traits by altering the genetic composition of a stock. Similar results may be obtained by hybridization, using two stocks of related species to produce hybrids possessing the desired properties. Webster and Flick (1975) demonstrated improved growth and survival after stocking interstrain hybrids of domestic and wild brook trout, but the heterosis appeared most pronounced when nonindigenous strains from Quebec were used for the wild parent (Webster and Flick 1981). The objective of producing a variety of salmonids close to the lake trout, capable of maturing and reproducing at an early enough age to avoid parasitism by the sea lamprey (*Petromyzon marinus*) in the Great Lakes, was achieved by producing the hybrid splake; selection was primarily on the basis of gas retention in the air bladder and early age at maturity (Berst et al. 1980).

Procedures for the deliberate production of inbred lines of brook trout and brown trout for use in hybridization studies were first described by Wright (1951–52). Such inbred lines may be used to study particular genes on a constant background, to remove deleterious recessive genes, and to produce heterozygotic hybrids exhibiting "hybrid vigor" (Ihssen 1976). In this regard, Moav et al. (1978) described the production of fast-growing domestic breeds of carp for crossing with and improving wild stocks. Standard reference lines of rainbow trout with precisely documented genotypes are now being developed for studying inheritance in that species (Kincaid 1979).

Hybridization has also been used for the production of monosex or sterile hybrids to be used in aquaculture where reproduction is undesirable. Pruginin et al. (1975) have reviewed the known means of achieving that aim in *Tilapia* species. Unisex *Tilapia* have also been produced by administering estrogens to induce sex reversal (Clemens and Inslee 1968; Hopkins et al. 1979). The creation of inbred lines has also been achieved by radiation-induced gynogenesis (Purdom 1969), and by cold shock inducement of polyploidy in plaice (*Pleuronectes platessa*) (Purdom 1972), in *Tilapia* species (Valenti 1975), and in brook trout (Lemoine and Smith 1980).

The anadromous salmonids, including Pacific salmons (*Oncorhynchus* spp.), steelhead trout (*Salmo gairdneri*), and Atlantic salmon (*Salmo salar*), have complex life cycles and behavioral patterns that generally prevent the use of captive brood stocks in their management. Egg collections for their culture must therefore be made from wild populations that are subject to natural fluctuations in environmental conditions. Successful management programs for these species are therefore highly dependent on maintenance of the genetic character of the wild stock being managed. This would apply also to the management of lake trout (*Salvelinus namaycush*) stocks, if eggs were collected from wild populations rather than from domestic brood stocks.

The relatively short period of time during which these species are maintained under controlled hatchery conditions reduces but does not necessarily preclude the possibilities for genetic selection. When the gametes are collected in the field, opportunities for change during captivity are minimal. However, some attempts have been made to alter the characteristics of wild stocks by holding them in the hatchery for the months required to rear them from the egg to smolt or yearling stage. Some of the earlier studies were made on chinook salmon (*Oncorhynchus tshawytscha*) by Donaldson and Menasveta (1961), who reported selection of spawning adults for improved growth rates, earlier age at maturity and spawning season, greater survival, increased tolerance of high temperatures, and resistance to disease. The time of return of winter steelhead trout was advanced following selection at a hatchery in Oregon (Rosentreter Peterson 1977), and efforts are being made in Washington State to increase the availability of salmon stocks to anglers by selecting several characteristics in those fish for enhancement by fish culture (Anon. 1972).

Attempts at transplanting various Pacific salmon stocks have often been unsuccessful (Ricker 1972), possibly because the transplanted fish were unable to home correctly. By crossing transplanted female pink salmon (*Oncorhynchus gorbuscha*) with males from the local river system, Bams (1976) obtained returns of adults 10 times greater than those of the pure donor stock planted in the same river; the difference was shown to be the result of improved homing ability. Thus, interstrain hybridization is perhaps a potentially important tool for management of some Pacific salmon species.

Few efforts have been made to select disease-resistant wild stocks of fish through breeding techniques. The attempts of Donaldson and Menasveta (1961), using chinook salmon, were noted above, but no specific diseases were mentioned nor were any results presented. Heritability estimates of the resistance of different stocks to vibrio disease in Atlantic salmon (Gjedrem and Aulstad 1974) and to infectious hematopoietic necrosis disease in sockeye salmon (*Oncorhynchus nerka*) (McIntyre and Amend 1978) indicate, however, that selective breeding against those specific diseases is possible.

Evidence of Unintentional Genetic Changes

The potential for the occurrence of unintentionally produced changes is greatest in stocks of fish that have been propagated for generations in fish culture facilities. The controlled artificial conditions and management practices used throughout the life cycle exert inadvertent selection pressures on the stock, or they remove natural selection pressures. Over successive generations, the stock becomes increasingly more adapted to the artificial rearing environment and less so to the natural environment from which it was removed.

Behavioral changes are generally noticed first. Vincent (1960) and Moyle (1969) observed differences in depth preference of brook trout in the laboratory. The wild stock stayed

nearer the bottom of the tanks whereas those that had been raised for generations in hatcheries tended to remain near the surface. Also, the hatchery fish were not frightened as easily as the wild fish. Flick and Webster (1962) raised the progeny of wild and domestic brook trout in the same hatchery and planted matching size groups in the same lakes. The domestic trout were more susceptible to being caught by fly-fishing and trap netting than their wild counterparts. In Israel, the Chinese big belly carp (*Cyprinus carpio*) was more adept at escaping seines than the European domestic race of carp (Wohlfarth et al. 1975; Moav et al. 1978). The Chinese carp has been cultured for hundreds of years longer than the European. Hybridization of the two stocks produced intermediate behavior and thus confirmed the genetic basis for the differences.

Unintended physiological differences between wild and hatchery-reared brook trout were demonstrated by Vincent (1960) in laboratory tests. He found that the wild fish could withstand higher water temperatures and greater concentrations of metabolites than the hatchery fish. The wild fish also exhibited superior stamina when tested in troughs, a characteristic also confirmed by Greene (1952). Dickson and Kramer (1971) similarly found reduced activity in hatchery rainbow trout after starvation as compared with their wild counterparts.

Genetically based differences in development between hatchery and wild stocks have been demonstrated in several studies comparing post-stocking performances of wild and domestic brook trout. Flick and Webster (1964, 1976), in a series of controlled stocking experiments comparing three wild and two domestic stocks, showed that survival and growth were superior in the wild groups. The wild fish and wild domestic hybrids also exhibited greater longevity, whereas the domestic stocks were more advanced in maturity. Possible differences in age at maturation were also indicated by the results of Fraser (1981), who compared survival and growth after stocking between two wild stocks and their hybrids and a single domestic stock. The wild and hybrid fish performed two to four times better than the domestic fish. Brown et al. (1981) discussed possible direct and indirect effects of hatchery rearing of lake trout, which may be responsible for a lack of successful reproduction in the wild.

Most of the examples cited above have consisted of observed differences between wild and domestic stocks of fish compared or tested under similar conditions. Recent studies using carefully designed breeding experiments have demonstrated the genetic basis of some of the observed differences. Also, electrophoretic techniques have been used to show clearly the genetic differences between wild and domesticated stocks (Ryman and Stahl 1980).

The majority of recent studies have been with rainbow trout. Aulstad et al. (1972) and Kincaid (1976 a, b) have shown reduced egg hatchability and survival of fry from swim-up to 150 d in inbred domestic strains of rainbow trout. Those studies also demonstrated clearly reduced growth rates and weightlength ratios attributed to inbreeding depression. Gall and Gross (1978) showed that poor fertility and small egg size were also evidence of inbreeding in rainbow trout. An examination of allele frequencies of the highly selected University of Washington stock of rainbow trout revealed a loss of genetic diversity in that stock relative to other stocks more recently established from wild populations (Allendorf and Utter 1979).

Allendorf and Phelps (1980) used electrophoretic methods to demonstrate inbreeding and genetic drift in a hatchery stock of cutthroat trout (*Salmo clarki*) compared with a wild stock native to the same area from which the hatchery stock was established. Those authors suggested that the loss of variability (indicated by a reduction in the number of alleles at a given locus) is likely to result in increased susceptibility to disease. Inbreeding and genetic drift were also identified in three hatchery stocks of brown trout compared electrophoretically with two wild populations in Sweden (Ryman and Stahl 1980). The same authors also compared the Swedish hatchery stocks with a Polish hatchery stock from which they were derived. The use of too few founding parents and genetic drift were postulated as causes of inbreeding (Ryman and Stahl 1981).

Data on genetic changes which may have occurred unintentionally are scarce for wild stocks which are subjected to fish culture practices for short portions of their life cycles and for which no brood stocks are retained in captivity. A few studies on Atlantic salmon stocks have indicated that the recapture of fewer hatchery-reared fish than wild fish (Carlin 1969) may be the result of inbreeding found in the former (Ryman 1970). Møller (1970) also concluded that the interchange of stocks and the use of hatchery propagation may have affected the gene frequencies of the original stocks. Saunders (1981) presented evidence for the loss of genetic diversity of Atlantic salmon stocks as a result of management efforts which include fish culture.

Ricker (1972), in an extensive review of the genetic and environmental bases for differences between Pacific salmon stocks, showed that a number of differences between stocks are genetically determined while many are environmentally induced. The only specific reference to the effects of hatchery rearing indicated that size of chinook salmon at a given age was intentionally increased by selective breeding. However, adaptation to hatchery conditions by one chinook salmon stock was given as a possible reason for better returns of a transplanted stock than of the native stock, in contrast with most transplants which were less successful. Helle (1981) noted the lack of documentation on stock transplants that were unsuccessful. He pointed out that genetic changes are likely to occur in salmon stocks when the young are raised to the smolt size without any natural selection in a hatchery. This may be more important with chinook, coho (*Oncorhynchus kisutch*), and steelhead which are raised beyond the fry stage in artificial conditions.

Altukhov and Salmenkova (1981) presented evidence at this symposium from electrophoretic studies that changes in allele frequencies can result from fish cultural practices if the local stocks under consideration are not sampled carefully and representatively for propagation purposes. These studies examined chum (*Oncorhynchus keta*), pink, and sockeye salmon stocks being managed under a fish culture and transplantation program. Returns of fish that originated from egg transfers were 5–10 times lower than those that were progeny of local stocks. With salmon species, and rainbow trout also, it has often been common practice for eggs and sperm to be collected from the middle of a spawning run when the fish are readily available at weirs. A representative sample should include collections from at least the beginning and end of a

run as well as its middle.

Environmental Effects of Fish Culture

The nongenetic effects of the artificial rearing environment in fish culture facilities on fish being reared for planting in the wild may have as much, or more, impact on the success of the stocking program as the unintended genetic changes. Such environmentally induced changes affect the phenotype of the stock, and are usually expressed in terms of a decreased fitness for stocking in the wild. The fitness of a stock determines its probability of survival to maturity to contribute genes to the next generation, and hence influences the genetic composition of the stock. In this manner, environmentally induced changes in the captive stock could indirectly affect the genetic variability of the native stock being managed.

Examples of the causes of environmentally induced changes are incubation at elevated temperatures during winter, artificial diets and feeding techniques, and the lack of appropriate exercise. The changes effected by these environmental conditions are difficult to distinguish from genetic changes. It is also difficult to measure their effects on the fitness of captive stocks. Webster and Flick (1981) obtained conflicting results in three experiments comparing wild stocks matured in a hatchery environment with domestic stocks raised in a natural pond, although statistically significant differences in fitness amount to only 10%. Research to identify and reduce or eliminate these detrimental effects is urgently needed. This need is especially evident in regard to evaluating the traditional methods of raising salmonids in the Great Lakes region and elsewhere. It is likely, however, that a balance will eventually be found between the use of environmental manipulation to reduce costs and simulation of natural conditions necessary for maximizing survival after planting in the wild.

Evidence for Environmentally Induced Changes

The "ideal" water for traditional salmonid culture is preferably ground water from a spring capable of providing more or less constant temperatures throughout the year. The temperature prevailing in a hatchery during the winter months would therefore be higher than ambient temperatures in the lakes or streams containing the populations of the species that are being managed. That difference has been regarded as advantageous because the higher temperatures accelerate incubation of the eggs and the early development of the hatched fry. Accelerated development during the early months enables the production of larger-sized fingerlings, smolts, and yearlings for stocking. Although there is conflicting evidence, particularly on anadromous species, it is generally believed that larger-sized fish at release generate higher returns. Higher ambient temperatures have therefore been utilized and sometimes even increased by heating to assist in speeding up growth. Some potentially negative effects of the elevation of temperatures, however, are only now being identified.

The effects of temperature and associated oxygen levels on development rate have been studied in brook and rainbow trout eggs and fry by Garside (1966a, b). The mean vertebral number in both species decreased with increased rate of development at higher temperatures. There was also an increase in the frequency of abnormal vertebrae at the higher temperatures. Garside postulated that these changes may be due to the rapid and large increase in oxygen requirements at hatching which was not being satisfied at higher temperatures. Balon (1980) observed the effects of temperature on the early development of the lake trout and noted differences in rate of calcification of the skeletal system and in the rate of heart beat and suggested that development of the respiratory system was better at 9.5°C than at 4.4°C.

Berst et al. (1980) found higher numbers of gill rakers and fin rays in the wild than in hatchery stocks of lake trout, brook trout, and their splake hybrid, whereas stocks with both wild and hatchery experience had intermediate counts. Higher vertebral counts also were found in splake from cooler more northerly locations. There was some circumstantial evidence suggesting that higher densities during rearing result in lower hard-tissue counts. The numbers of pyloric ceca were also higher in fish from the wild than fish from hatcheries. Artificial diets may be responsible for that difference and indeed at one hatchery where more ground beef liver is fed the numbers of pyloric ceca were correspondingly higher.

The acceleration of smolt development by the use of elevated temperatures results in precocity in some anadromous salmonids. Bilton (1978) found that larger coho smolts produced a greater percentage of jacks (precocious males) of larger size which in turn reduced the production of returning adults. Bilton and Jenkinson (1980) further reported returns of normally reared coho smolts 14 times as large as the returns from accelerated juveniles. MacKinnon and Donaldson (1976) had found earlier that elevated water temperatures produced a higher proportion of precocious smolts in pink salmon, but they also suggested that a combination of photoperiod and a critical size might influence the development of smolts. Prolonged exposure to an extended photoperiod was shown to inhibit growth and smolting in coho and sockeye salmon (Clarke et al. 1978) and elevated water temperatures increased the percentage of precocious steelhead in eight Idaho hatcheries (Schmidt and House 1979).

Both temperature and photoperiod were clearly identified as influencing the smoltification process in a recent review of the environmental factors affecting smoltification of anadromous salmonids by Wedemeyer et al. (1980). Those authors discussed the effects of water temperature on the osmoregulatory mechanism and the development of ATPase activity during smolting, and pointed out that both direction and rate of change of day length were important cues in the process. It was suggested that elevated water temperatures be used cautiously to avoid shortening the process of smoltification and that smolts be held outside without lights in order that they be exposed to the natural photoperiod and light intensities.

Artificial diets and feeding techniques and schedules all affect the behavior and consequent survival of hatchery fish following stocking. Rainbow trout reared in a hatchery on dry pelleted diets and ground liver were both found to have inadequate glycogen reserves and a lowered resistance to fatigue compared with wild fish (Miller et al. 1959). The pelleted feed was nevertheless superior to the ground liver. Artificial feeding techniques may produce accelerated growth, the disadvantages of which were discussed earlier for anadromous salmonids. The preference for staying near the water surface

shown by hatchery fish accustomed to artificial feeding (Vincent 1960; Moyle 1969) may render them incapable of the correct feeding response after release in the wild as well as making them vulnerable to predators (Fraser 1974). Sosiak et al. (1979) found that Atlantic salmon parr reared in a hatchery feed less effectively than wild parr for at least 2 mo. after release. The larger size of the hatchery parr indicated that size-dependent food selection may have occurred, but feeding experience and rearing habitat differences were considered to be responsible for the observed difference.

It is well-known that deficiencies in artificial diets cause various nutritional diseases. For example, a deficiency of vitamin C causes scoliosis, and an imbalance of dietary zinc can cause cataracts in rainbow trout (Ketola 1979). Gjedrem (1976b) found flesh color to be somewhat heritable, but the carotenoid content of a diet has a strong influence also (Bauernfeind 1976). It has also been suggested that the proportion and types of fat in artificial diets have a strong influence on survival following planting by providing differing energy reserves for the period of adjustment to searching for food, although research in this area has only recently begun.

The possibility that a lack of appropriate exercise for fishes in cultural facilities leads to reduced stamina has often been raised. Stamina of wild rainbow trout, rated by measuring swimming duration in a current of fixed velocity in a tunnel, was greater than that of hatchery-reared trout (Horak 1972). Differences in stamina in sockeye salmon raised by different rearing methods were observed by Bams (1967), but similar differences were shown to be genetically based in rainbow and steelhead trout (Tsuyuki and Williscroft 1977). Semiwild rainbow trout had better relative swimming ability than the deeper-bodied domestic rainbow trout in studies by Thomas and Donahoo (1977), although it was not clear whether the differences observed were environmental or genetic. Studies by McNeish and Hatch (1978) also found stamina tunnel tests on Atlantic salmon parr to be inconclusive. Increased current, and therefore swimming speed, may promote accelerated smoltification, although little is known about optimal currents for smoltification (Trump and Leggett 1980).

The lack of correct imprinting just prior to and during the parr–smolt transformation in hatcheries has often been cited as a cause of subsequent straying in anadromous stocks. Accidental imprinting to a wrong location may also occur. Artificial imprinting of presmolt coho salmon with morpholine and phenethyl alcohol prior to release proved quite effective (Horrall 1981). Attempts to imprint sockeye and pink salmon fry with morpholine and decoy the returning adults to nearby streams were unsuccessful in Alaska (W. R. Heard, National Marine Fisheries Service, Alaska, personal communication).

The use of antibiotics for disease therapy and prophylaxis were shown to have unexpected effects on coho smolts prior to their release into seawater (Bouck and Johnson 1979). Higher mortalities were observed after treatment with Formalin and nifurpirinol and to a lesser extent with copper sulfate, potassium permanganate, malachite green, quaternary ammonium compounds, and heavy doses of MS-222. The effects were mitigated by holding the fish in freshwater for 4 d following exposure.

Rearing densities may have serious detrimental effects on fish in intensive fish culture. Juvenile chinook held at high densities in the laboratory exhibited a supression of normal ATPase development (Strange et al. 1978). Returns of Atlantic salmon adults released as smolts from a hatchery in Maine were found to be related to water flow and also to rearing density during the last few months in the hatchery (Hosmer et al. 1979). These factors were among only 5 found significant out of 85 variables examined by regression analyses. A reduction in rearing densities for coho salmon smolts resulted in higher returns of adults in British Columbia (F. K. Sandercock, Department of Fisheries and Oceans, Vancouver, British Columbia, personal communication).

Fin erosion and descaling often result from handling during fish culture procedures. Bouck and Smith (1979) experimentally removed 25% of the scales of coho smolts and observed a 75% mortality during 10 d in seawater, although none held in freshwater died. Other stresses which can occur as a consequence of fish culture practices are usually the result of poor management (Wedemeyer et al. 1976).

Recent research efforts have begun to show that some of the incubation equipment commonly in use in salmonid hatcheries may have detrimental effects on developing fry. Bams (1972, 1979) constructed gravel incubators designed to simulate natural conditions for pink salmon. Whereas hatcheries normally produce four times the number of adults per unit of eggs, fry to adult survival is usually supressed compared with wild stocks. The use of gravel incubators resulted in survival of fry to adult comparable to a naturally propagated stock. Bams postulated that artificial rearing conditions result in a delayed mortality of inferior stock. It has also been suggested that the provision of support by gravel or other artificial substrates such as Astro-turf and plastic saddles may be advantageous for the development of sac fry (Bailey and Taylor 1974; Leon 1975).

It should be clear from the foregoing discussion that fish culture techniques considered to be successful because they may produce higher numbers of fish or larger sizes for planting in the wild may not always be appropriate to management goals. The side effects of manipulating environmental conditions can instead be highly detrimental to the objective of the stocking program.

Methods for Identifying Genetic Changes and Environmental Effects on Captive Stocks

To develop means of avoiding undesired changes that occur in captive stocks, those changes must first be recognized and identified. Careful experimental design is of course a vital element in any approach to distinguishing between genetic and phenotypic changes in stocks caused by the fish culture environment. Without deliberate experimentation, including proper controls, the two different types of change that occur may be inseparable from each other. For some brood stocks, such experiments may run for several consecutive years. Facilities for separating different experimental and control lots must be available.

All experimental studies must of course measure the effects of any "treatment" on the resulting phenotype. The term treatment is here used in a statistical sense and may refer to genetical or environmental factors or to the interaction between them (genotype environment interaction). The most basic, and perhaps most common, problem is to determine

whether a phenotypic effect is caused by environmental or genetic factors, or both. The next step is to determine the relative importance of these sources of variation.

It is not until recently that fish culturists appear to have become fully aware of the need for thorough experimental design when testing for and estimating the relative importance of various factors. In this respect, fish breeders in general have been much slower than most of their colleagues in other fields of animal breeding to adopt current techniques of experimental design and statistical evaluation. One reason for this lag may be that it is (or has been) more difficult to perform unambiguous experiments with fish than with terrestrial species, which have been domesticated for a long period of time. For instance, the fact that fish are restricted to water brings about some immediate problems when an investigator wants to perform a test in replicate which may require two ponds instead of one. The fact that most hatcheries are constructed for production purposes only, i.e. frequently consisting of just one or a few large ponds that must be used as efficiently as possible, further increases the problem. On the other hand, many characters in fish are strongly influenced by various environmental factors, which often make the need for carefully controlled experiments greater in fish than in other organisms.

Imagine, for instance, the situation where an investigator wants to test the effect of two temperatures on growth. He may put fish with identical genetic background (e.g. the same stock) at equal densities in two containers with different water temperatures and compare the growth patterns. This is a typical example of a poor experimental design; in the absence of replicates (i.e. two containers for each temperature), little can be concluded from possible differences in growth patterns in the two containers. The existence of additional (undetected) environmental differences that affect growth can never be ruled out, even if experimental conditions are controlled carefully; replicates are needed to provide an estimate of the variation within each treatment (temperature). On the other hand, the four containers needed for a valid experiment may be used more efficiently in the same experiment to test whether the effect of temperature is identical in different stocks. In this case "stock" is used as one treatment and temperature as another; the experiment is designed as a two by two factorial analysis and both stocks are tested in both temperatures. Using a slightly different statistical testing procedure, additional information may be obtained if specimens from different stocks are identified (e.g. through tagging) so that fish from both stocks can be tested in all four containers.

Analysis of the phenotypic variation between and within full sib families reared under similar conditions has frequently been used to estimate the relative importance of heredity and environment on some character. The results from this kind of experiment have often been misinterpreted because of a lack of replicates. In such cases the investigator has ignored the fact that the full-sibs reared together not only have genes in common but also have shared a common environment all their life. As a result, the relative importance of the hereditary component may have been dramatically overestimated. It is also true that the questions meant to be answered in many of those experiments would have been more properly addressed from analyses of half-sib families instead of full-sibs.

The fact that many fishes produce large numbers of eggs and sperm which can be easily handled permits refined breeding schemes and advanced experimental designs. The interested reader is referred to Becker (1975), Falconer (1964), or Sokal and Rohlf (1969) for examples of detailed descriptions of computational procedures and discussions on the theoretical aspects of experimental design. Hybridization studies (Ihssen 1976) and the use of standard reference lines (Kincaid 1979) may also be used in particular to examine genotype environment interactions and to distinguish between the genotypic and environmentally caused differences.

Regardless of the experimental design chosen, results must be measured by an examination of the phenotypes produced. The relative usefulness of traditional and more recent methods in this context are compared in Ihssen et al. (1981) and need not be repeated here.

Recommendations for Brood Stock Management

In addition to the following recommendations, those of both the F.A.O./U.N.E.P. Working Group on the Conservation of Genetic Resources of Fish (Soule 1981) and the International Symposium on Fish Gene Pools (Ryman 1981) are strongly endorsed. In essence, every effort should be made to prevent potentially detrimental genetic changes caused by the rearing of fish for rehabilitation programs in the artificial environments of fish culture facilities.

1) Accumulate standard information about basic population genetics of wild fish stocks for use by those in charge of managing captive fish stocks. Included in this recommendation is the need to re-examine existing data on stock differences to see if there is evidence of clear differences between hatchery stocks and those in the wild from which they were derived. All the stocks being reared for Great Lakes fisheries rehabilitation programs should be clearly characterized and compared with those existing in the wild. In special situations, genetic markers might be introduced to distinguish between the cultured and the wild stocks to ascertain the relative contributions to recruitment.

2) Maintain native fish stocks still existing in natural ecosystems where possible, in those water bodies.

3) In situations where the stresses on the environment are such that a stock is not likely to survive in its original ecosystem, consider the establishment of reference populations in natural habitats or in "refuge lakes." These refuge lakes must be as similar as possible to the original environment of the stock. The reference stocks therein may serve as "gene banks" for checking against unintended changes that may occur in captive stocks derived from the original wild stock. However, it must be remembered that if the refuge lake has similar conditions to the original lake it too is likely to have its own native stock. In that case, a choice must be made as to which stock is the more important to maintain, considering all of the characteristics of each. It is also important to appreciate that the reference stock itself will probably undergo changes in a water body which is unlikely to be an exact duplicate of that from which the stock was rescued.

4) Following the identification and characterization of fish stocks, choose those most closely approximating what was known of depleted or lost stocks before embarking on fish culture programs for their rehabilitation. This may include the use of several stocks combined in a single stocking program

to maximize genetic variability.

5) Develop protocols for the continuing collection of systematic records on brood stocks. These protocols should involve the use of all available monitoring and measuring techniques that will identify changes as they occur (e.g. electrophoresis) as well as environmentally caused changes (e.g. vital statistics, physiology, behavior). In order that the causes of such changes can be determined, records of stock life history, genetic background, environmental information, details of mating procedures and dates, egg production and quality, incidence of diseases, and other factors must be maintained.

6) To conserve the genetic character of stocks being managed by fish culture, develop and implement techniques on the basis of the lastest theory and existing knowledge. Apart from reducing unnecessary deliberate selection, new scientific techniques must be applied along with existing fish culture techniques, primarily to slow down the rate of inbreeding in captive fish stocks. Some of these methods are listed below, roughly in order of the most effective and preferred methods first. (a) In establishing brood stocks or maintaining anadromous runs of salmonids, random sampling to obtain the founding parents is essential (Ryman and Stahl 1980). The sampling must cover the range of sizes, ages, spawning times, and sites of the spawning parents. (b) As far as possible, use large effective populations of captive brood stocks and random mating procedures in the propagation of brood stocks in fish culture stations. The minimum number of parents used should be 50 of both sexes (Ryman and Stahl 1980). (c) Techniques such as rotational line crossing so long used by plant and animal breeders should also be introduced in fish culture stations. Kincaid (1977) has described an example using rainbow trout. (d) Periodic infusions of genetic material from wild stocks may be considered as a means of maintaining genetic variability, although this practice carries with it the risk of introducing diseases (Brown et al. 1981). (e) The new techniques of gamete preservation and transfer may become more important tools in fish culture as they are refined. Spermatazoa from chinook and coho salmon have already been preserved by freezing (Ott and Horton 1971) and ova or embryos may also be preserved in the future. (f) Hybridization between different stocks, breeding between generations, and exchange of stocks or gametes between facilities may all be considered as means of improving genetic variability in captive stocks.

7) Agencies must encourage the application of sound experimental designs and techniques for identifying and measuring the magnitudes of genetic and environmental effects in fish culture. Because of the lack of such a scientific approach in the past, reasons for the failure of production facilities to achieve their objectives have often remained unknown. Funds should be provided for use as selected production facilities in conjunction with research laboratories to assess the effects of differing water qualities (e.g. temperature, pH, hardness), artificial diets and feeding techniques, rearing numbers and densities, unit designs, flow characteristics, pressure and depth, the timing of imprinting, and other conditions. The results of such studies should then be applied to modify the design of production facilities with due consideration to reducing artificial selective pressures or detrimental physiological changes resulting from fish culture practices.

8) The need to retain increased numbers of brood stock lineages and additional experimental groups of fish will require greater capacity for subdivision of lots within fish culture stations than has been the general practice among agencies in the Great Lakes region. Only by providing a greater number of smaller units within each production facility can the essential studies be conducted on the genetics, physiology, behavior, growth, and disease transmission of cultured fish stocks. Laboratory and tagging equipment will also have to be upgraded at most existing facilities.

9) For more efficient experimental management of specific stocks, an increased number of smaller, more versatile fish culture stations should be provided, as close as possible to those water bodies that contain the target stocks.

10) Finally, maintain and extend educational programs and information exchange among researchers, fish culturists, and fisheries managers. Only through such exchanges can the practical use of existing and new knowledge be applied to reduce the effects of detrimental changes in artificial rearing environments.

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Genetic Aspects of Fisheries Rehabilitation Programs[1]

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The stocking of indigenous or exotic fish species is often a desirable aspect of fisheries rehabilitation programs. Two strategies are proposed for the choice of fish for stocking. The first plan involves making separate collections of fish from each of several genetically different populations, performing all possible crosses between the different sources, and then stocking the progeny. In contrast to selective breeding programs, this strategy maximizes genetic variability and then relies on the environment for the selection of the most appropriate genotypes. The second plan is to sample populations from waters environmentally similar to those being rehabilitated that may contain preadapted genotypes. Application of this strategy should consider the use of gene banks or natural refugia as a source of preadapted genetic variability. When gene flow may occur between stocked fish and local populations, the second strategy should be used in favor of the first to minimize the impact on native gene pools. When choosing fish to implement either strategy, it is important to know the distribution of genetic variability within and between populations to sample adequately the variability present.

Key words: stocking, genetics, fisheries, rehabilitation, natural selection, exotic introductions, genetic introgression, gene banks, Great Lakes

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Dans les programmes de réhabilitation des pêches, il est souvent désirable de stocker des espèces de poissons indigènes ou exotiques. Nous proposons deux stratégies de choix de l'espèce à ensemencer. La première comporte la collecte séparée de poissons de chacune de plusieurs populations génétiquement différentes, effectuant entre les différentes sources tous les croisements possibles, pour ensuite ensemencer la progéniture. Contrairement aux programmes de croisements sélectifs artificiels, ce plan porte au maximum la variabilité génétique et compte ensuite sur l'environnement pour la sélection des génotypes les plus appropriés. La seconde stratégie repose sur l'échantillonnage de populations provenant d'eaux ambiantes semblables à celles qu'on veut réhabiliter et qui peuvent contenir des génotypes préadaptés. Si l'on adopte cette stratégie, il faudrait envisager l'utilisation de banques de gènes ou de refuges naturels comme sources de variabilité génétique préadaptée. S'il y avait probabilité d'échanges géniques entre les poissons stockés et les populations locales, on devrait opter pour la deuxième stratégie afin de minimiser l'impact sur les pools de gènes indigènes. Pour

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échantillonner adéquatement la variabilité, il est important, dans le choix de l'espèce à ensemencer selon l'une ou l'autre stratégie, de connaître la distribution de la variabilité génétique intra et interpopulations.

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ALTHOUGH many freshwater fishery environments have been disrupted by processes such as acid precipitation, point source pollution, hydroelectric power development, overfishing, and exotic introductions, some have occasionally become sufficiently restored to permit the rehabilitation of fisheries with indigenous or exotic species. Successful environmental restoration has, in turn, provided a unique opportunity for fisheries biologists to formulate and execute management plans to reestablish viable fisheries. Management initiatives that address ecologically extrinsic factors affecting fish populations are crucial to the success of rehabilitation programs and may take the form of habitat modification, prevention of habitat degradation, and fisheries regulations. These extrinsic factors, however, must be considered in combination with the intrinsic genetic factors of the fish populations to be manipulated. Recently, fishery scientists and managers have become increasingly aware of the importance of genetics in fish restoration and management (e.g. Calaprice 1969; Ihssen 1976; Utter et al. 1976; Smith et al. 1976; Moav et al. 1978; Allendorf and Utter 1979; Ryman and Ståhl 1980; Soulé 1980).

In this paper, we describe two rehabilitation strategies to use in choosing fish for stocking, discuss their rationale and implementation, and present some specific management applications. We have developed the strategies with special consideration for the fisheries of the Great Lakes, although the principles we consider may have general application for other freshwater fisheries.

Strategies for the Choice of Fish for Stocking

In waters that have been partially restored and are suitable for rehabilitation, formerly abundant fish species often have been lost or exist at low densities. As a result, the planting of either indigenous or exotic species is usually contemplated for most rehabilitation programs. The choice of fish for transplantation or for use as brood stock in hatcheries thus becomes an important consideration prior to the execution of stocking programs.

Fish cultural practices have historically involved some type of selective breeding, either planned or inadvertent. Intentional selection in hatcheries has often focused on single traits such as growth, color, shape, and disease resistance (e.g. Wolf 1953; Donaldson and Olson 1955; Toney and Bowen 1968). Because of the nature of such selective breeding, viability of hatchery fish may be reduced through a loss of genetic variation (Ryman 1970; Kincaid 1976; Allendorf and Utter 1979; Allendorf and Phelps 1980; Ryman and Ståhl 1980). We believe that the amount of genetic variability present within stocked fish may be a key factor in their potential fitness, i.e. their capacity to survive and reproduce in the existing environment. This fitness derives from a combination of many heritable traits that cannot presently be genetically partitioned and identified. As we cannot predict appropriate genetic combinations, it is best to resist the temptation to construct specialized genomes through artificial selection for stocking purposes.

Outlined below are two strategies for choosing fish to be used for rehabilitation stocking. The first strategy is to make collections from wild populations that represent the entire genetic diversity of the species, perform all possible crosses within and between the different sources, and then stock the progeny. This strategy maximizes genetic variability, and after stocking relies on the wild environment for selection of the most fit. This scheme is designed to increase the chances of stocking some fish with the proper genetic combination that will survive and reproduce in the newly restored waters. By holding wild fish only as long as required to make the crosses and raise the progeny to suitable (preferably very young) planting size, this plan should minimize inadvertent and potentially adverse hatchery selection. In some circumstances it may be best to continue to hold the parents in the hatchery to produce additional first-generation progeny in later years. This scheme should maximize the genetic diversity within the planted fish, provided that an adequate sample of the genetic variability within the species has been made. This strategy should not be used where the potential exists for interbreeding between stocked fish and indigenous populations. Such hybridization would break up previously existing and potentially adaptive gene combinations that occur in the wild populations.

The second strategy is similar to the first except that fish are chosen only from populations that occur in environments similar to those where stocking will occur. This plan should increase the possibility of success by using the end products of a history of selection similar to that which may occur in the waters to be stocked. The gene combinations successful within the donor populations hopefully will demonstrate similar fitness after transplantation. Sources of such preadapted fish may be from natural refugia within the restored waters or from outside the drainage basin. For example, the rehabilitation of lake trout in the Great Lakes might use trout from Lake Superior Shoal (a refugium) or from a large Canadian lake such as Great Bear Lake. These fish may be preadapted to the Great Lakes as a result of similar environmental pressures. The main difficulty with this alternative strategy is whether the perception of environmental similarity by the biologist will be the same as that of the fish. Although the first strategy is intended to ensure that some fit genotypes will be present among the stocked fish, the most adaptive genotypes may be only a small proportion of the planted fish. Use of the second strategy should increase this proportion.

In some waters suitable for rehabilitation efforts, irreversible habitat alterations have occurred and/or the community structure has markedly changed. In such cases, these waters may represent a unique environment found nowhere else in the geographic range of the species. The first strategy, which uses the entire genetic diversity of a species, is probably best for fisheries rehabilitation of such waters.

In other situations, the aquatic environments either have not been seriously altered or appear to have been restored to preexisting conditions. A species may be depleted or absent only in a local area, while populations occur in adjacent areas. The second strategy, which uses preadapted fish from the adjacent populations, should be chosen for the fisheries rehabilitation of such waters. If gene flow occurred historically among populations in these waters, then the donor populations may possess much of the genetic information that previously existed in the depleted population. Use of such preadapted genetic variability should enhance chances for successful rehabilitation and minimize the genetic impact on the adjacent populations from subsequent gene flow. Caution is advised in the use of the second strategy in areas of broad access, e.g. Pacific salmon returning to North American streams from the open ocean (Helle 1981). Transplanted stocks may not "home" accurately and problems with introgression may occur (Bams 1976).

Genetic Rationale and Implementation

Fundamental to the strategies discussed above is the premise that genetic variability within the stocked fish will be related to their overall fitness (survival and reproduction) in the new environment. During the early development of population genetics theory, Fisher (1930) recognized that the amount of genetic variation is positively correlated with the rate of evolutionary change by natural selection. This relationship is stated as the fundamental theorem of natural selection: the rate of increase in fitness of a population at any time is equal to its genetic variance in fitness at that time. Simply stated, genetic variability is the "stuff" on which evolutionary change depends (Lewontin 1974). Without genetic variability, stocked fish may be unable to adapt to new or changing environmental conditions.

Experimental evidence for the positive correlation between the amount of genetic variation and the rate of adaptation of populations has been provided by Ayala (1965) for the fruit fly, *Drosophila serrata*. Two populations were bred so that one population initially had about twice as much genetic variation as the other. The populations were then allowed to "evolve" for 25 generations with intense competition for food and living space. During this period, both populations became gradually better adapted to this environment; however, the population that had the greater initial variation had a substantially faster rate of evolution as measured by its rate of population increase.

Implementation of the proposed strategies should take advantage of the existing genetic variation in the species of interest. Genetic variation in natural populations can exist at two fundamentally different levels of organization: within and between local populations. The total amount of genetic variation in a species can be estimated and subdivided into these two components by an examination of allelic frequencies using the technique of gel electrophoresis of proteins (Allendorf and Utter 1979) and the method of analysis presented by Nei (1975). This approach has been applied to rainbow trout (*Salmo gairdneri*). This species contains more electrophoretically detectable genetic variation than other closely related species of the genera *Salmo* and *Oncorhynchus* (Allendorf and Utter 1979). The total genetic variation in rainbow trout of the Columbia River drainage, for example, has been 'partitioned' into a within-population component of 92.2% and a between-population component of 7.8% (Allendorf and Phelps 1981). Thus, the great majority of the genetic variation in these fish results from differences between individuals within populations. Other fish species show a similar distribution of genetic variation, i.e. a relatively low amount of genetic variation between populations, for example, bluegill (*Lepomis macrochirus*; Felley and Avise 1980) and striped bass (*Morone saxatilis*; Sidell et al. 1980). In contrast, other species exhibit substantial genetic differentiation between populations, for example, brown trout (*Salmo trutta*; Ryman et al. 1979; Ryman and Ståhl 1981) and cutthroat trout (*S. clarki*; Loudenslager and Gall 1980).

Knowledge of the distribution of genetic variability within and among populations is necessary to collect fish that adequately represent the variability available for either strategy. If most of the genetic variability of a species is present within each population, then collecting fish from only a few populations will suffice. Conversely, as the amount of genetic differentiation increases between populations, fish from more populations must be included to obtain a satisfactory sample of the variation. In addition, the second strategy requires that care should be taken within the breeding program to preserve the parental genotypes as adaptation may be in the form of the original gene combinations and their interactions.

In addition to knowing the distribution of genetic variability, it is important to collect a large number of individuals from each population to obtain an accurate representation of the genetic variability within populations. Much of the discussion on effective population size given by Ryman and Ståhl (1980) is pertinent to this issue and will not be repeated here. In general, to minimize the sampling errors of founder effects, the number of parents used from each donor population should be greater than 50 for the first strategy and 100–200 for the second strategy (1:1 sex ratio).

Management Applications

Fish stocking as a management activity for rehabilitation can be divided into three general categories: introduction, reinforcement of remnant natural populations, and "put-and-take" fisheries. The discussion that follows addresses the choice of genotypes used and the genetic dangers inherent in each of these stocking practices.

The objectives of introduction stocking are to establish self-sustaining naturally reproducing populations of fish. This type of stocking includes intentional exotic introductions such as rainbow trout to Australia (MacCrimmon 1971) and reintroductions such as Atlantic salmon (*Salmo salar*) to Lake Ontario (Christie 1972).

Exotic introductions are by definition transplantations outside the normal range of the species; thus the use of preadapted genotypes as discussed previously is less likely to be possible since habitats and communities of donor and receiving waters will probably be different. In this case, the best approach is to introduce fish that represent as much of the genetic variability of the species as possible (the first strategy). Dangers in the introduction of exotics are well known, and considerable thought should be given to the possible ecological consequences of such stocking to the

structure and function of the community within the receiving waters (e.g. kokanee, *Oncorhynchus nerka*, introduced to Lake Tahoe, Morgan et al. 1978). A potential genetic danger in exotic introductions is interspecific introgression, as isolating mechanisms may not exist between formerly allopatric species. This problem has been particularly evident between planted rainbow trout and indigenous cutthroat trout in North America (Behnke 1972).

Reintroductions of formerly indigenous species may succeed by either strategy for the choice of fish to stock. The decision of which strategy to use will be dependent on the biologist's or manager's perception of the ecological conditions of the restored waters. For example, in Lake Ontario in addition to substantial changes in the habitat, several major species have become extinct or greatly reduced, leaving the lake mainly populated with exotics, notably rainbow smelt (*Osmerus mordax*) and alewife (*Alosa pseudoharengus*) (Christie 1972). On the basis of the uniqueness of the habitat and community, the best chance for stocking success with Atlantic salmon may be to use fish that represent as much as possible of the total genetic variability of the species.

Other waters may be environmentally similar to conditions prior to perturbation, and the use of preadapted fish (second strategy) may speed the rehabilitation process. In some instances before extirpation, representatives of a species have been transplanted and preserved in hatcheries or other lakes, i.e. artificial or natural gene banks (Hynes et al. 1981). For example, before extinction lake trout from Lake Michigan were stocked in Green Lake, Wisconsin, where they now probably represent the only surviving remnant gene pool of Lake Michigan lake trout (Hacker 1956). Fish from gene banks may represent an unusual opportunity to use preadapted genotypes for reintroductions.

Reinforcement of remnant natural populations is the second category of fisheries management rehabilitation activities. The objective in this rehabilitation is to rebuild populations to acceptable abundance levels that will then be maintained by natural reproduction. In this case, a remnant of the original gene pool still exists within the system. Since it is difficult to assess the genetic importance of the remnant, we believe the best approach is to assume that it represents an important resource of preadapted genetic variability and therefore should receive high priority for preservation (see Soulé 1980).

If the remnant population is of sufficient size to serve as a gamete source, then the rehabilitation strategy of using preadapted genetic variability should be followed. An example would be the use of Superior Shoal lake trout for stocking purposes in Lake Superior, as previously discussed.

If the size of the remnant gene pool is insufficient to serve as the only gamete source and it must be supplemented, hybrids between the local native source and a donor source are a possible alternative. A few local males are capable of fertilizing many donor females, and the hybrids will possess a portion of the previously successful genotypes. Such hybrids sometimes have dramatically increased fitness as compared to the pure donor source (Bams 1976). The donors should be taken from nearby sources, preferably from ones with which the stock being rehabilitated may in the past have exchanged genes.

The genetic variability extant in remnant populations, however, may not represent the amount that was formerly present. Insight into the degree of variability that previously existed may be provided by historical evidence of past population structure (e.g. Goodier 1981; Brown et al. 1981). When outside sources of fish are deemed desirable then natural or artificial gene banks and environmentally similar waters are the best sources of fish for stocking. The major danger in this circumstance is intraspecific genetic introgression between the introduced and native populations (Calaprice 1969; Krueger and Menzel 1979; Allendorf et al. 1980). Genetic swamping of native gene pools from external sources of fish would represent a loss of locally adapted genetic resources. Prevention of such hybridization may be possible by incorporating into stocking methodologies knowledge about the isolating mechanisms between populations (Horrall 1981).

The third category of rehabilitation stocking is "put-and-take" fisheries. Different from the other two management activities, this type of management depends on using hatcheries as artificial extensions of spawning and rearing habitat. "Put-and-take" stocking has been used for indigenous species that, as a result of limited or nonexistent spawning habitat, are unable to maintain population levels required to make exploitation feasible (e.g. Cayuga Lake lake trout management, Webster 1959). In this case, gametes for hatchery use would be best obtained from the local natural populations (second strategy) so as to benefit potentially from preadapted genetic variability. Managers who plan to use exotic species in "put-and-take" fisheries should consider the previous discussion on exotic introductions. A genetic danger in put and take stocking of either type of fish is introgression between hatchery fish and native populations. The planting of sterile fish would prevent genetic introgression and is feasible since reproductive fitness is unimportant.

Summary and Conclusions

Fundamental to the strategies proposed for the choice of fish for rehabilitation stocking is a recognition of the unpredictability of the fitness of the animals planted. Since the genetic factors of fitness are multiple and interactive, it is difficult to create fit genomes through artificial selection. Artificial selection for single traits also reduces genetic variability. Rather than reducing genetic variability, our first strategy is to choose fish that represent as much of the genetic variability of the species as possible, to perform crosses within and between populations, and to plant the progeny. By maximizing the possible genetic combinations, it is hoped that by chance some will be fit for the new environment and will, therefore, disproportionately contribute to the gene pool of subsequent generations. The second strategy is to sample from populations that exist in waters that are environmentally similar to those being rehabilitated and which may contain preadapted genotypes. A higher proportion of fit genotypes may occur among stocked fish by following this alternative. Where the danger exists of genetic introgression with local native populations, the second strategy should be used to preserve existing genetic resources.

To apply these strategies, the process of choosing populations to sample from depends on a knowledge of the distribution of genetic variability in the species. Descriptions of genetic variability, within and between populations, are a prerequisite to implementation, but unfortunately are lacking

for many species. Further research efforts should be directed toward this goal. Studies on population structures in unperturbed areas may be particularly valuable in that they will allow comparison with the structure of new populations established. The electrophoretic studies on brown trout and other salmonids in Sweden (Ryman and Ståhl 1981) represent an example of such research. In the tropics, before the genetic variability in populations can be described, basic taxonomic studies will be required (Soulé 1980).

Rehabilitation management should include programs for monitoring the genetic effects of stocking activities. These will be particularly important where remnant populations occur and the danger of genetic introgression with the stocked fish exists. The use of genetic tags in planted fish (Allendorf and Utter 1979; Schweigert et al. 1977) provides a means for the rapid detection of hybridization. Early detection of introgression would permit the development of alterations in stocking methodologies that could preserve the genetic integrity of remnant populations.

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A Wild Salmon, Trout, and Char Watch: An International Strategy for Salmonid Conservation[1]

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This paper elaborates an international strategy to register and monitor stocks of wild salmon, trout, and char through the Holarctic region. The urgent need for such a watch has been emphasized by the increasingly international nature of environmental pollution and stress (e.g. acid precipitation), and the fact that several local 'watch-like' schemes have recently arisen independently in different countries. The main objective of a watch is to foster the conservation of distinct species and stocks of wild salmonids and their habitats by an international program of monitoring and information exchange. At intervals a global wild salmonid status report would be produced for public release. The watch would be developed through an international network of interested parties and organized by a steering committee, probably set up within an existing international organization.

Key words: wild salmon, trout, char, watch, worldwide strategy, stock conservation

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Nous décrivons dans l'article qui suit une stratégie internationale de compilation et de surveillance des stocks de saumons, truites et ombles sauvages dans toute la région holarctique. Une telle surveillance devient de plus en plus urgente par suite de la nature de plus en plus internationale de la pollution et des contraintes (p. ex. précipitation acide) imposées à l'environnement et du fait que plusieurs initiatives locales de « surveillance » ont récemment vu le jour indépendamment dans divers pays. L'objectif principal de ce programme est de favoriser la conservation d'espèces et de stocks distincts de salmonidés sauvages et de leur habitat par une surveillance et un échange d'information à l'échelle internationale. De temps à autre, un rapport global sur la condition des salmonidés sauvages serait publié à l'intention du public. Le programme devrait être mis en place par l'intermédiaire d'un réseau international de groupes intéressés et organisé par un comité de direction, probablement formé au sein d'un organisme international existant.

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THE importance of fish stocks as fundamental reproductive entities in the conservation and management of the fisheries of the Great Lakes has been convincingly demonstrated by evidence presented at the Stock Concept International Symposium. From syntheses and recommendations developed from these various papers, future management programs for the Great Lakes will have a realistic base in fish genetics as well as in population dynamics. However, the principles of stock conservation and management developed for the Great Lakes have implications far beyond their shores: the purpose of this paper is to present a proposal, based on the same principles, for the development of a worldwide strategy for the conservation of salmonid stocks in many countries throughout the northern hemisphere.

The Stock Concept International Symposium was one of several initiatives during 1980 with objectives related to conserving and preserving various valued taxa. These initiatives are occurring at all levels of jurisdiction from fully worldwide to small locales of a few hundred hectares, and the scientists involved worldwide must number in the thousands.

The various initiatives that characterize this "movement" may be classified into three broad types: (a) High-level commitment to the guiding principles of the movement, which have been made in national and international forums by senior politicians of many countries. (b) Conceptual, scientific, and technical aspects as addressed by many agencies, institutions, and organizations. (c) Practical programs that have been implemented, often by modifying existing programs of narrower scope, in a variety of jurisdictions within many countries, and in a few instances at international levels.

Although these various initiatives have not all been well integrated, the nature and extent of political commitments already made, the depth and breadth of technical and conceptual understanding, and the practical experiences with many growing programs are all sufficient to engender optimism that major progress will be made during the 1980s.

The most recent and comprehensive initiative on this subject was the FAO–UNEP Expert Consultation on the Conservation of Genetic Resources of Fish attended by one of the authors (PSM), which met in Rome in June 1980 (Soule 1980). In addition to describing earlier efforts, the FAO–UNEP group concluded that increased practical measures towards "genetic resource preservation" were justified on the basis of human nutritional benefits, economic benefits such as biomedical substances and the aquarium trade, and ecological benefits, in which valued fish species can serve as effective and efficient indicators of the status of entire aquatic ecosystems. It should be noted that these experts deliberately restricted their consideration to benefits more or less closely related to economic well-being or "progress" as conventionally implied. Two further types of justification may be added: social groups in some countries rely directly on fish as food and in cultural ways, and there exist values related to cultural opportunity and social equity; many persons throughout history have recognized that humans should not knowingly extinguish any but the most dangerous life forms, a concern that might be labeled as related to environmental harmony and nature-oriented ethics.

All of these justifications, but particularly the latter two, are not visionary or far-fetched. A careful examination of what is coming to be recognized as 'optimal management' in many places will reveal that many of the justifications listed above come into play in determining allowable catches and the allocation of the catch among different interests. Fisheries workers who seek to advance programs of genetic resource preservation should take precautions against being caught in a web of too narrow justification. In particular, short-term economic considerations should be balanced by longer-term cultural, social, and natural values.

Creation of an International Watch

With all the above as historical context and practical justification, the authors propose the creation of an international wild salmon, trout, and char watch, an idea originally suggested by Regier and Power (1979) and Regier (1980). The watch would form an international network of concerned and committed people at various levels from local to worldwide. The focus on wild salmon, trout, and char relates to the fact that in various countries and international regions there are already underway activities related to these taxa that approximate what we consider to be characteristic of a "watch."

The initial purposes of a network would be to exchange information of various kinds, and this would likely stimulate improved effectiveness and efficiency of existing programs and perhaps contribute to the emergence of new undertakings elsewhere. It might also lead to some international standardization of, for example, survey design, sampling techniques, and data summarization.

Before proceeding with further discussion of some desirable organizational features of an international watch, it is useful to review the numerous organizations to which such a watch will necessarily need to accommodate itself. For simplicity, the term 'wild salmonid watch' is used as a general term.

The Institutional Setting

Existing regional programs have originated from one or a collaborating set of a variety of organizations, which may be classified according to four broad types: scientific and scholarly, public interest and concern, professional, and governmental. Each of these types relates to some efforts already underway with respect to the preservation of wild salmonid taxa.

a) Scientific organizations relate to multi-disciplinary national academies within countries, to disciplinary international associations within the International Council of Scientific Unions (ICSU), and to somewhat more practice-oriented governmental or international bodies such as the United Nations Educational Scientific and Cultural Organization (UNESCO). Examples can be found of aquatic programs that have emerged from each of these three subgroups.

b) Public groups with a concern about "environmental harmony" often relate to environmental or naturalist organizations, which peak in the International Union for the Conservation of Nature and Natural Resources (IUCN). This organization has recently formulated a World Conservation Strategy which emphasizes genetic resource preservation.

Other interests are served by such organizations as Trout Unlimited and the World Wildlife Fund; these are increasingly involved in programs of taxon conservation.

c) Fisheries professionals in North America have worked under the auspices of the American Institute of Fisheries Research Biologists (AIFRB) and the American Fisheries Society (AFS) to advance the cause of fish species preservation in North America. AIFRB (1975) has had an impact in Alaska in this respect (see below). The AFS committees related to endangered species and to environmental concerns have developed policy positions consistent with our interests in a wild salmonid watch.

d) Most successful major programs related to the preservation of fish taxa now have strong governmental involvement. Sometimes, as with the Endangered Species Act in the USA, the governmental agency involved may have a strong mandate. More usually, governments collaborate with one or more of the three types sketched above to advance the cause of taxon preservation, and sharing of activities among the collaborating groups seems to be highly variable.

Watch-like programs already underway have evolved or emerged from a variety of different concerns, values, policies, and organizations. Such diversity is interesting and challenging, but the programs all have the objectives of conserving genetic and ecological diversity, evolutionary and ecological taxa, a spectrum of genetic resources, and the natural habitats in which these thrive. The question of whether some international organization already exists and with which a salmonid watch could associate itself must be considered.

Firstly, there is no worldwide association of fisheries scientists within the ICSU or any other family of organizations. This is also the case with respect to fisheries professionals. In North America both the AFS and AIFRB are serving most of the needs of professionals, but neither has a sufficiently broad geographical base to serve as the parent organization for an international salmonid watch.

Specific activities of the Fisheries Department of FAO often provide settings for fisheries workers to address broader issues. UNESCO, UNEP (United Nations Environment Program), and FAO increasingly collaborate on issues related to efforts like a watch, but the public interest groups play practically no role. Also FAO has no formal mandate to take the lead in fostering something like the watch envisioned here.

IUCN is a union of sovereign states, government agencies, and nongovernmental organizations whose main purpose is to "promote or support action that will insure the conservation of nature and natural resources on a worldwide basis, not only for their intrinsic cultural or scientific values but also for the long term economic and social welfare of mankind. The Union considers that conservation is best defined as the rational management of the earth's resources to achieve the highest sustainable quality of living for mankind." One hundred countries are represented in IUCN, which is the world's only independent scientific organization dealing with the conservation of nature and natural resources.

Thus an appropriate institutional connection for a salmonid watch would appear to be IUCN's Survival Service Commission (SSC), especially SSC's Freshwater Fish Group. Interactions with IUCN on the subject of the watch suggest that its interests might be well served by close collaboration. Following the oral presentation of this paper at STOCS, one of the authors (PSM) and the Chairman of SSC's Freshwater Fish Group (Mr. A. C. Wheeler) held a meeting at which it was agreed that a salmonid watch could find a logical role within this Group, which is at present being reorganized and developing its activities worldwide.

Foundation Studies

In several different parts of the northern hemisphere, schemes already exist which fulfill several of the requirements of a watch. For the most part these appear to have originated spontaneously, sometimes under the auspices of government-funded organizations and sometimes as a result of the enthusiasm of a private individual. Though they vary in details, all have arisen essentially because of an increasing international realization of the threats to wild salmonid stocks and to the vulnerable habitat which they occupy.

It is appropriate here to review a few of the relevant schemes which could form the local bases for an intergrated international scheme. There are undoubtedly others, in various parts of the Holarctic area, which are relevant in one way or another.

Salmon in Alaska

Since the beginning of this century, artificial propagation of salmon has been practiced to supplement declining natural stocks. Early attempts at salmon culture in Alaska were unsuccessful, largely because of lack of knowledge of the biological requirements of various species. These early hatcheries were abandoned, but recent advances in knowledge of nutrition, disease, juvenile life history, and especially incubation substrates make artificial propagation of salmon an appealing method for increasing the abundance of salmonid fishes. This new knowledge has revived the interest in hatcheries in Alaska (Helle 1981). However, transplantation of stocks and other applications of this technology could result in unfavorable changes in the genetic composition of some wild salmon, trout, and char stocks (cf Ricker 1981).

The ability of salmon to return to their natal streams for spawning is well documented. This "homing instinct" results in genetic adaptation to the specific environment encountered by each stock. Thus, different stocks display numerous variations in behavior, morphology, and ecological requirements. Characteristics like size and age at maturity, time of spawning, and migratory behavior of juveniles and adults have been shown to be strongly under genetic control. These and many other heritable features are adaptive to the particular environmental experience of each stock. Thus, every stock is genetically different, and transplanted stocks may upset the critical genetic characteristics of native stocks.

The Alaska District of the AIFRB has recommended that: (1) Enhancement of rehabilitation of the salmon stocks in a stream or lake system should be accomplished using the native stocks already present in the system. (2) In the special situation where transplantation of brood stocks is the only alternative, careful consideration should be given to selection of the donor stock. In addition, an evaluation of the success of the transplant should be mandatory. (3) Hatchery stocks should be separated (in space and time, or both) from wild stocks, both in the fishery and on the spawning ground. (4) If

isolation of hatcheries is unacceptable, then certain areas should be designated as gene banks to protect the genetic diversity of the wild stocks. Artificial propagation would not be allowed in these areas, and special consideration would be given to prevent overfishing and environmental degradation. (5) A standing committee with representatives from academic, government, and private sectors should be formed to provide planning, evaluation, and recommendations concerning strategies for protecting the genetic diversity of wild stocks. This committee should oversee the transplantation of stocks, hatchery techniques, and other methods of enhancement. Members with special training in genetics would be an essential part of this committee.

Brook Trout in the Southeast USA

There is considerable watch-like activity concerning brook trout in the southeast of the USA (as far north as West Virginia). Every state containing reproducing brook trout populations is working on, or has completed, recent surveys determining distribution of this species. The situation is basically the same as reported at the Brook Trout Symposium (Estes et al. 1978). Specific information about the surveys can be obtained from agencies in states containing brook trout waters (West Virginia, Virginia, North Carolina, Georgia, Tennessee, and Kentucky).

In addition, the Forest Service, during the land management planning process, is selecting "indicator species" to monitor habitat changes. Where wild brook trout populations occur, they will be the indicator species, unless an endangered species occurs there also. This process should provide an ideal opportunity to implement part of the "salmonid watch."

Salmonids in Ontario

Desiring to prevent the further deterioration of fisheries in Ontario because of habitat changes, overfishing, and invasion of nonnative species (Loftus and Regier 1972), fisheries management agencies have developed a holistic framework for fisheries in Ontario called Strategic Planning for Ontario Fisheries (SPOF) (Loftus et al. 1978). This treatise advocated two societal goals for fisheries.

1) To protect and maintain healthy aquatic environments and associated fish communities, and to rehabilitate those now degraded, in order to ensure continued supplies of fish and fishing opportunities that in part satisfy society's requirement for (a) wholesome food, (b) employment and income, (c) recreational activity, and (d) high quality of the human environment.

2) To create public awareness of the importance of healthy fish communities and aquatic ecosystems, and to engender a harmonious pattern of uses of fisheries resources and the terrestrial and aquatic ecosystems on which they depend.

Further, the agencies stated that one major issue is the need to recognize that when a stock of fish becomes rare or extinct, this is a clear sign that the human environment is deteriorating also.

In the spirit of these goals and issues, the Ontario government has recognized the need to identify and protect susceptible salmonid stocks and habitat. Lakes with self-sustaining populations of lake trout (*Salvelinus naymaycush*) have received special recognition (Martin and Olver 1976), including the undertaking of special pollution control measures more stringent than the norm. Similarly, fisheries managers have become more demanding in their requirements to protect stream habitat for salmonids including brook trout (*S. fontinalis*), rainbow trout (*S. gairdneri*), and brown trout (*S. trutta*). As well, significant resources have been committed to habitat restoration and fish stock rehabilitation in Ontario, though clearly such projects must have a clear scientific base (Fraser 1981). Responses are monitored regularly within a selected subset of waterbodies called assessment units and by monitoring stations in fishways on large Great Lakes tributaries.

The American Lake Trout in the Great Lakes

The loss of lake char habitat and stocks from the Great Lakes area has been well documented (Goodier 1981, Dehring et al. 1981, Brown et al. 1981). In a recent paper by Ryder et al. (1979), an ecosystem objective for the Laurentian Great Lakes was defined on the basis of the fundamental life requirements of a single species, the American lake trout. This ecosystem objective is to attain and sustain the maintenance of an appropriate oligotrophic environment to perpetuate a cold-water community of indigenous organisms. Within this community, reproducing, genetically diverse stocks of lake trout will be the top predators and therefore the primary controlling compartment of the steady-state community. Implicit in this objective would be the understanding that optimal harvests of lake trout and other species may be taken by various user groups in proportion to their different internal production rates, without a marked alteration of either the community integrity or its level of steady-state yield (internally, production processes will accelerate, age structure will change, and other density-dependent factors will come into play). Also implicit within the objective is the condition that the various vertebrate and invertebrate species within the biotic community will be contaminant-free (according to standards established by the Great Lakes Water Quality Agreement of 1978), and the harvested segment shall constitute a palatable and safe food product for human consumption.

The rationale for using lake trout as an indicator organism follows from its wide distribution in the Great Lakes Basin, it is a top predator, it has well-documented niche characteristics and habitat requirements, and is of major anthropocentric concern. Details of niche and habitat were described and synthesized from a Great Lakes perspective, A methodology for the determination of the level of success in achieving the ecosystem objective is proposed through the monitoring of certain output properties of the Great Lakes ecosystem. Ultimate analysis is achieved through the application of holistic concepts to information. Annual feedback of ecosystem information to regulating agencies allows for appropriate management of the aquatic system through the use of mitigation or rehabilitation procedures.

Wild Trout and Arctic Char in Sweden

Monitoring of char in Sweden started in the 1940s in relation to hydroelectric developments there. At the moment, several important projects are funded by federal agencies. The

National Swedish Environment Protection Board sponsors a project monitoring the amount and distribution of genetic diversity among natural and hatchery populations of various salmonids: this is one of the most advanced international projects within the salmonid watch concept and it is aimed at identifying the populations within each species that should be given priority with regard to conservation activities. Some aspects of the work have recently been described by Ryman and Ståhl (1981). Another important project arose after it became obvious that acid precipitation was having a serious effect on the ecology of freshwater habitats in Sweden (Dickson 1975), and a test fishing procedure was designed and initiated there in 1972.

As the waters of southwest Scandinavia were endangered because of their low natural buffering, and there still remained important stocks of arctic char and brown trout, it was decided that 36 lakes known previously to contain stocks of char should be investigated. A joint program between the State Fisheries Board of Sweden (SFBS) and the State Environment Protection Board of Sweden (SEPBS) was intended to cover as many factors as possible. Water chemistry, phytoplankton, and zooplankton communities were studied by the SEPBS, and the fish communities by SFBS through the Institute of Freshwater Research at Drottningholm.

The lakes were fished with survey gillnets with a standard range of mesh sizes at fixed stations and seasons. The following basic data were collected on a regular basis: (1) fish length and weight, (2) age (calculated from scales and otoliths), (3) catch per unit effort, and (4) water samples, pH levels, temperature profiles, and other standard limnological measurements. The initial results showed that: (1) char is an excellent indicator organism. Several lakes containing char have become devoid of that species because of a rapid decrease in pH. Today only 25 of the lakes have populations; (2) the relations between fish species have changed; for example, roach (*Rutilus rutilus*) is the first to disappear, after that salmonids, and finally perch (*Perca fluviatilis*); (3) acidification seems mainly to affect reproduction, as the first sign of change is the appearance of fast-growing fish belonging to a few year-classes.

Another reason to choose char as an "indicator organism" is the fact that there exist many sibling species and stocks, which respond differently to environmental stresses. It is therefore reasonable to refine the identification of the "char complex," and to try to map the zoogeography of individual stocks. It is also important to realize that char are not only sensitive to pollution, but to other human activities, such as exploitation, hydro-power development, afforestation, fish introductions, recreation, etc.

Char in the British Isles

There is, as yet, no integrated scheme equivalent to a salmonid watch in the British Isles, but a number of relevant activities have taken place here in recent years. The mapping of populations of this (and other freshwater) species was initiated in the mid-sixties (Maitland 1972) and more recently conservation prescriptions were promoted (Maitland 1979). In Scotland, several ecological studies have been carried out (e.g. Campbell 1979) and a registry of known stocks has just been completed (Maitland et al. 1981). In Ireland, the status of char has been reviewed by Went (1945) and others. In England, char of the Lake District (especially Windermere) have been studied (e.g. Frost 1978), while in Wales, the threat to one of only three existing populations (in Llyn Peris) has resulted in an attempt to start new populations (A. Rogers personal communication). In the British Isles as a whole, several populations have become extinct over the last 200 years, and recent threats from acid precipitation and other pressures have emphasized the need for a watch.

Operational Objectives

The objectives of individual schemes vary, but overall there are many features in common. The major operational objectives of the salmonid watch are clear and may be defined as follows, with respect to self-sustaining wild species and stocks, wherever they occur:

1) To foster conservation, preservation and rehabilitation of: distinct species and stocks; genetic resources; diversity of taxa; sufficient appropriate habitat.

2) To exchange information on ongoing programs that address the above objective.

3) To confer on ways in which particular programs might be improved.

4) Where desired at the level of individual programs, to work towards comparability of data.

5) To confer on the processes by which watch concerns and information are transferred into practice.

6) To produce at intervals a global wild salmonid status report for public release.

Enabling Objectives

It is clearly in the interests of a salmonid watch for it to be linked with an existing international organization. As already noted the most appropriate parent body may be IUCN. The enabling objectives of the watch consistent with the operational objectives above are as follows: 1) To establish an international steering committee; 2) to establish a one-person directorate/secretariat with continuing access to secretarial/clerical assistance; 3) to establish a global communications network to include representatives of existing programs and other committed experts; 4) to plan and convene a global symposium/workshop within a few years; 5) to attract sufficient funding to support the international watch network and process.

Discussion

The early years of a salmonid watch will be directed towards establishing the global network through the international steering committee. Much of this period will be devoted to the communication of information and ideas among the individuals and groups involved. Ideas for coordinated monitoring schemes with specific aims and objectives will be explored and initiated, where practicable. In particular, proposals related to the arctic char — the only salmonid found across the entire Holarctic region — will be given serious consideration for an experimental, harmonized, global,

monitoring scheme. Where possible, local fisheries will be involved in such studies (e.g. the Inuit people of northern Canada).

It should be made clear that, in part, wild salmonids are being used in the present strategy as indicator organisms. Thus the attempt is not only to conserve these salmonid species as representative of distinct genetic stocks (Utter 1981) for their own sake, but also as useful early warning indicators of the general state of the environment from an anthropocentric point of view. The habitat requirements of char and other salmonids are rigorously more demanding that those of many other fish species. Therefore, by protecting these wild salmonids, most other cohabiting species are also automatically preserved. The same objective would not be achieved by using carp (*Cyprinus carpio*) in this role.

In Sweden, the roach is apparently the first fish species to disappear following acid stress. It could be suggested that this might be a preferable indicator, compared to char. However, the roach is of restricted distribution in northern Europe and rarely occurs in unbuffered waters. This makes it much less valuable than char in this context. However, local systems of monitoring should clearly not be too inflexible, and if a part of any community of fishes that includes salmonids is more sensitive to a particular stress, then that organism should also be used as an indicator. Thus in the Great Lakes of North America it is intended to use other organisms as indicators beside lake trout (R. A. Ryder personal communication). Prime candidates are the walleye (*Stizostedion vitreum vitreum*) and the mayfly *Hexagenia* for Lake Erie, and the crustaceans *Mysis* and *Pontoporeia* for the pelagic–profundal regions of Lake Superior and Lake Huron.

In North America a variety of citizen–action groups has assumed responsibility for protecting and improving local streams. Save Our Streams (SOS) and Trout Unlimited (TU) encourage local citizens to work with landowners, municipalities, and resource management agencies to ensure salmonid streams are preserved, aquatic habitat is protected, and where needed, necessary rehabilitation of habitat and fish communities is undertaken. These activist groups ensure that agencies consider the value of streams within local and regional planning schedules. Secondly, the citizens become "watchdogs" and can be more efficient than fisheries staff in ensuring that sensitive salmonid habitat is not destroyed. Thirdly, these groups provide a free-volunteer labor force that can undertake many jobs presently beyond the resources available to management agencies. In essence, these citizens are part of a salmonid watch. Elsewhere, there are environmental groups concerned with the Great Lakes (Great Lakes Tomorrow, etc.), and similar groups occur in Europe. There is no doubt that an international exchange of experiences and ideas in these fields could prove fruitful.

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The Stock Concept, Discreteness of Fish Stocks, and Fisheries Management[1,2,3]

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MacLean, J. A., and D. O. Evans. 1981. The stock concept, discreteness of fish stocks and fisheries management. Can. J. Fish. Aquat. Sci. 38: 1889 – 1898.

This paper examines the concept and definition of fish stocks and the processes that influence discreteness of these stocks in light of the tactics necessary for the application of the concept in management. Two approaches to the definition of stocks are discussed. These differ in the extent to which management inputs other than biological ones are considered. We consider definition to be less important than the adoption and development of a stock concept to provide a genetic perspective for fisheries management. The two central levels of the stock concept — the subdivision of species into local populations and the adaptive nature of genetic differences between these populations — are discussed with respect to the interlinked set of ecological and genetic processes that result in subdivision and determine the discreteness of these stocks. Genetic discreteness usually implies some restriction of gene flow, and spatial and temporal mechanisms of isolation are discussed with examples from the STOCS symposium. The structure of subdivided populations is seen as the result of behavioral processes that are one component of a set of coadapted traits, which collectively constitute a life history strategy. The necessity for managers to develop a new integrated view of species, which incorporates both ecological and genetic arguments, is discussed.

Key words: stock concept, life history, gene flow, ecological and genetic discreteness, local adaptation stock management

MacLean, J. A., and D. O. Evans. 1981. The stock concept, discreteness of fish stocks and fisheries management. Can. J. Fish. Aquat. Sci. 38: 1889 – 1898.

On trouvera dans l'article qui suit une analyse du concept et de la définition des stocks de poissons, ainsi que des processus qui influent sur la discontinuité de ces stocks en regard des tactiques nécéssaires à l'application du concept à la gestion. Nous considérons deux approches de la définition des stocks. Ces approches diffèrent selon l'importance que l'on accorde aux incidences, autre que biologiques, de la gestion. La définition, à notre avis, importe moins que l'adoption et la mise au point d'un concept de stock qui fournirait à la gestion des pêches une perspective génétique. Nous jetons un regard sur les deux paliers centraux du concept de stock — la subdivision de l'espèce en population locale et la nature adaptive des différences génétiques entre ces populations — en fonction d'un ensemble de processus écologiques et génétiques, liés entre eux, responsables de la subdivision et de la discontinuité de ces stocks. La discontinuité génétique comporte ordinairement une certaine restriction du flux génique. Nous examinons les mécanismes spatiaux et temporels d'isolation à l'aide d'exemples tirés du colloque sur les stocks. Nous considérons la structure des populations subdivisées comme étant le résultat de processus comportementaux, éléments d'un ensemble de caractéristiques coadaptées, formant collectivement une stratégie de cycle biologique. Nous discutons en dernier lieu de la nécessité, pour les gestionnaires, de former un concept nouveau et intégré de l'espèce, incorporant des arguments à la fois écologiques et génétiques.

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UNTIL recently, fisheries managers have had their hands full with the problems of management of single species of fish in the waters for which they were responsible. As a result of conferences such as SCOL (Loftus and Regier 1972), PERCIS (Colby 1977), the Stock Identification Workshop (Simon and Larkin 1972), and the present STOCS symposium, managers are faced with the intimidating prospect

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that they will need to consider simultaneously a more general ecosystem level of ecological resolution and a finer stock level of population biology in their decisions. In essence, managers are being advised that they require further understanding of the structure and dynamics of the systems that they manage if their actions are to be effective.

The purpose of this paper is to examine the stock concept and the processes that influence discreteness of stocks in light of the tactics necessary for the application of the concept in management. We will pay particular attention to the implications of differences between species life histories for management of stocks.

The Problem of Stock Definition and the Stock Concept

A fundamental problem for fisheries managers is the definition of stocks for management. Altukhov (1981) points to the lack of agreement, which was echoed at the STOCS symposium on the definition of objects of study and management at and below the level of species. This terminological confusion reflects both the diversity of ways in which gene pools are structured and the hierarchical nature of these structures. For example, many salmonids home to natal spawning streams, which results in genetic discreteness of local populations separated by small distances, while bluegills (*Lepomis macrochirus*) in large reservoirs appear to be panmictic (Avise and Smith 1974, Altukov and Salmenkova 1981). Sockeye salmon can be grouped on the basis of management areas (Ricker 1981), or rivers (Ricker 1972), or lakes along a river, or spawning streams (Altukhov and Salmenkova 1981), or even redds along a stream (LeBar 1971). Rates of homing and straying can be defined for each of these groups to define the structure of the gene pool. The application of current biochemical, cytological, immunological, morphological, and ecological techniques permit us to subdivide any such assemblage of organisms into groups that range from one or two individuals to the complete assemblage (Ihssen et al. 1981b). The term stock has been used in various management contexts with little or no genetic content. What then is the basis for definition of stocks for management?

Two approaches have been advocated to solve this problem. Ihssen et al. (1981b) define a stock as 'an intraspecific group of randomly mating individuals with temporal or spatial integrity.' They argue that this biological definition represents a model against which presumed stocks can be compared and that current uses of the term stock by managers can be included under this definition. Larkin (1972) explicitly included the element of management feasibility in his definition of a stock as 'a population of organisms which, sharing a common gene pool, is sufficiently discrete to warrant consideration as a self-perpetuating system which can be managed.' Both definitions contain genetic and ecological requirements which must be met, but they differ in the extent to which management considerations other than biological ones enter into the definition of stocks.

We consider that the definition of stocks is not as important for management as the adoption of a stock concept to provide a genetic perspective in management decisions. Decisions can be made at several levels, so that, for example, sockeye salmon (*Oncorhynchus nerka*) harvest could be regulated on the basis of management areas, while the habitat of individual spawning streams is protected and restored. What appears to be required for effective management is sufficient information on both population structure and the processes that influence ecological and genetic discreteness so that managers can make the inevitable compromises between concerns related to emergent population properties, such as genetic diversity and local adaptation, and the socioeconomic returns from the fishery (Loftus 1976).

The Stock Concept and Discreteness of Fish Stocks

The stock concept has two central arguments: that fish species are subdivided into local populations and that there are genetic differences between local populations which are adaptive. If managers are to include genetic considerations in their decisions, they will need information on the biological differences between discrete local groups of a species, and they will need to understand the genetic and ecological processes that influence discreteness. For example, environmental changes such as dams and pulp mill effluents (Ryder 1968) may cause changes in gene flow which in turn can cause two stocks to merge or differentiate further. The process of genetic drift in small exploited populations can produce similar results (Speiss 1977). A clear understanding of the structure of the gene pool is a prerequisite for evaluation of management options, and Ihssen et al. (1981b) review several techniques to obtain the necessary information. This section of the paper will briefly summarize our current understanding of the ecological and genetic processes that result in subdivision and influence discreteness, with examples chosen from the STOCS symposium and the literature that focus on Great Lakes species and problems. In essence, we will elaborate the two central arguments of the stock concept mentioned above.

Process Influencing Stock Discreteness

The discreteness of a group of fish is a dynamic property that results from interactions between ecological and genetic processes in stochastic environments. Ecological discreteness results from spatial and temporal heterogeneity in the distribution of resources. Genetic discreteness depends on several evolutionary forces, including gene flow, mutation, genetic drift, and natural selection. It is difficult to discuss this set of interlinked processes, and what follows in this section is the bare outline of a complex argument (Wilson 1975).

Gene flow is defined here as the movement and establishment of genes and gene complexes into allochthonous gene pools (Endler 1977). Gene flow can thus be distinguished from migration, the long-distance directed movements of groups of individuals, and dispersal, the generally random, nondirectional movements of individuals, as neither of these latter processes will necessarily lead to exchange of genes, though essential to it.

The dispersal of many fish species is spatially restricted by a variety of geographical, ethological, and ecological barriers. Thus, most lake trout (*Salvelinus namaycush*) in Lake Superior do not move far from their spawning shoals or streams (Eschmeyer 1955; Loftus 1958). Similarly, most rainbow trout remain within 30 km of their spawning streams

in western Lake Superior (Biette et al. 1981). Tagging data suggest that whitefish in the Great Lakes and Lake Simcoe have a restricted dispersal (Casselman et al. 1981; Ihssen et al. 1981a), and that a similar pattern exists for walleye (*Stizostedion vitreum vitreum*) (Olson et al. 1978). Some individuals of these species move considerable distances, and the patterns of movement suggest that dispersal is leptokurtic, with higher numbers moving very small and very large distances than would be expected if movements were random (Endler 1977).

Although there are few measures of gene flow in natural fish populations, gene flow is probably spatially restricted compared to dispersal. Movement between areas will not always result in gene flow for at least four reasons:

1) Individuals that move may be less likely to spawn successfully because of behavioral incompatibility, failure to locate spawning and feeding sites due to lack of experience, and failures to obtain a spawning territory. MacLean et al. (1981) suggest the hypothesis that recognition of stock characteristics is a phenotypic assortative mating mechanism that increases the cohesiveness of lake trout stocks.

2) Individuals that move, particularly just prior to spawning time, may have insufficient energy reserves for reproduction and may also be in spawning condition at an inappropriate time.

3) Individuals that move must be genetically compatible with residents. Coadapted genes may be efficient at eliminating specific genetic variants introduced into the group that tend to lower adaptedness (Speiss 1977).

4) Introduced genes are initially rare and may be lost as a result of chance.

Reproductive homing of fish, the return to the natal site to spawn ('natal homing'), will obviously restrict gene flow, although few unequivocal demonstrations of this behavior exist outside of anadromous salmonids (Hasler 1966; Ricker 1972; Thorpe and Mitchell 1981; Horrall 1981). Repeated return of adults to the same, but not necessarily the natal, spawning site has been demonstrated for numerous species, including walleye (Olson et al. 1978; Colby and Nepszy 1981), lake trout (Eschmeyer 1955; Loftus 1958; Martin 1960; MacLean et al. 1981), white bass (*Morone chrysops*) (Hasler et al. 1969; Horrall 1981) and smallmouth bass (*Micropterus dolomieui*) (MacLeod and MacLean unpublished data). This latter behavior would tend to result in the potential for greater gene flow than natal homing.

The result of these geographic, behavioral, genetic, and ecological restrictions to gene flow is that fish species are subdivided into more or less separate subpopulations or local populations, as has been demonstrated in several papers at this symposium (e.g. Altukov 1981; Casselman et al. 1981; Ryman and Ståhl 1981). These local populations can be shown to be discrete through a combination of morphological, biochemical, cytological, and ecological analyses (Ihssen et al. 1981b). The patchy distribution of ecological resources such as food and spawning substrates intensifies this pattern of subdivision, because it amplifies the geographic and ethological barriers to gene flow. The effects of distance and patchiness are particularly important in large rivers and lakes, but homing can apparently lead to the development of discrete local populations in small lakes (Helle 1981; Ryman and Ståhl 1981; Kirkpatrick and Selander 1979).

The genetic discreteness of local populations depends on the interaction of gene flow, mutation, selection, and genetic drift (Wright 1969a; Speiss 1977). Subdivision of populations has several benefits, including favoring adaptation to local environments through selection, increasing total genetic variation by establishment of different genotypes in different locations, and favoring new combinations of genes through processes such as epistasis and genetic drift (Wright 1969a; Cavalli-Sforza and Bodmer 1971).

Local Adaptations of Fish Stocks

Wright (1929) long argued that selective processes are most effective if populations are subdivided into local populations, and several presumptive examples of adaptation to local environments were discussed at the STOCS symposium:

1) Altukhov (1981) attributes the low returns of chum salmon (*O. keta*) after eggs were transferred between rivers to local adaptation of stocks. Ricker (1972) summarized several transplant experiments with salmonids and concluded that survival to maturity was almost invariably reduced.

2) Helle (1981) discussed the behavioral studies of inlet and outlet spawning stocks of sockeye salmon, rainbow trout (*Salmo gairdneri*), and cutthroat trout (*S. clarki*). The movements of progeny of these two groups in order to reach the lake has been shown to be in part genetically controlled.

3) Utter (1981) reported on studies of Yellowstone cutthroat trout which revealed physiological differences between populations in widely different environments and the detrimental effects of introduced salmonids on the native interior cutthroat trout.

4) Saunders (1981) discussed the evidence that genetic differences between local populations of Atlantic salmon (*S. salar*) were adaptively related to environmental differences, and also that stocks differed in their resistance to vibrio, a bacterial disease. Power (1981) felt that many of the differences in life history patterns, which are assumed to be partly genetic (Ricker 1972; Thorpe and Mitchell 1981), of Atlantic salmon populations were adaptations to the environments of natal spawning streams (Schaffer and Elson 1975). Riddell and Leggett (1981) provide evidence that heritable morphological differences between local populations of Atlantic salmon in two spawning streams were due to adaptations to stream flow. Differences between local populations may thus explain the failure of planted Miramichi fish to recolonize New England rivers and the subsequent success with residual native populations (Saunders 1981).

5) Philipp et al. (1981) reported that different phenotypes of largemouth bass (*Micropterus salmoides*) reacted differently to thermal effluents and suggested that clines in phenotypic frequencies may reflect adaptations to local environments. However, observed correlations between spatial and temporal changes in phenotypic frequencies and some environmental characteristic must be treated cautiously — they can be explained by more than one hypothesis (Ihssen et al. 1981b).

6) MacLean et al. (1981) reported on differences in returns of stocks that were planted in lakes Opeongo and Simcoe, and they attributed the differences in survival to coarse-grained features of the environment such as water chemistry.

7) Lindsey (1981) and Brown et al. (1981) discuss situ-

ations where differences between phenotypes were related to the occupation of discrete ecological niches.

Our understanding of, and evidence for, adaptation to local environments is in each case indirect. The subject deserves further study, as it must be the basis for management definition of stocks and strategies for utilization and preservation of genetic variation. Loftus (1976) argues that maximum production of young salmon in complex river systems is achieved only when a complex of stocks is present, and local adaptation of subpopulations will, in general, result in coadapted gene systems with maximum fitness. Levene (1953) and others have shown that allelic variants can be maintained in populations, leading to greater genetic diversity and, thus in a sense, preadapting the population to future evolutionary change, if different alleles are favored in different habitats. Levins' (1968) analysis suggests that the way in which a population is adapted to environmental heterogeneity depends on environmental "grain," the relative frequency of environmental "patches," and the fitness of genotypes in each patch (Richmond 1978).

Local Adaptation and Gene Flow

A central assumption in many fisheries studies is that adaptive differences between local populations cannot be maintained if even small amounts of gene flow occur. Allendorf et al. (1981) examine the effects of gene flow and genetic drift on allelic frequency divergence among local populations, under the assumption that natural selection has negligible effects on allelic frequencies. Their model suggests that genetic discreteness is a function of the absolute number rather than the proportion of migrants, which is often what fisheries biologists have been obliged to measure, and also that significant allelic divergence will often be present despite substantial gene flow. Strong selection will maintain discreteness despite considerable gene flow, and these effects are amplified if migrants tend to reproduce in adjacent local populations, as most of the exchange will be between genetically similar groups (isolation by distance).

Gene flow does not, therefore, have a 'swamping' influence on processes such as selection and drift that can lead to differentiation, but it has at least three effects in subdivided populations (Speiss 1977): (1) it introduces new alleles and is, thus, a new source of variation analogous to mutation in local populations; (2) it increases the effective population size and, thus, reduces the potential for fixation of alleles; (3) it allows local populations to adjust to environmental change by utilizing new variability or by sifting it out if it lowers fitness. Gene flow can, thus, be viewed as a vital link between local populations which allows the species to expand and to explore diverse niches.

The dangers inherent in subdivision of fish populations are that inbreeding and genetic drift will lead to fixation of genes, loss of viability, and ultimately extinction of local populations. Stresses such as exploitation may augment these dangers through effects on effective population size. Random drift in small isolated populations will generally be nonadaptive (Wright 1969b), but drift can also be beneficial as it prevents too strict adherence to the effects of directed pressures that can limit genetic plasticity, and it also provides the conditions for rapid evolution. The pattern of connectedness, in terms of gene flow, between local populations thus simultaneously tends to increase fitness by adaptation to local environments and reduce fitness due to random processes.

To recapitulate, a variety of barriers result in the subdivision of the gene pool of a fish species into a number of more or less discrete local populations. The discreteness of these populations depends on a set of ecological and genetic processes that interact to adapt the population to local environments. The result of these processes is increased production through adaptation to diverse ecological niches, an increased capability to respond to environmental change through the maintenance of genetic diversity, and the tendency for new combinations of genes to arise as a result of epistasis and drift.

Spatial and Temporal Restriction of Gene Flow

Genetic discreteness of local populations implies a restriction of gene flow, although discreteness can be maintained by selection despite considerable genetic exchange, as discussed above. Although gene flow can be restricted by a variety of geographical and biological isolating mechanisms, we will focus on spatial mechanisms, due to natal homing and to distance, and temporal mechanisms, due to differences in spawning time that range from days to years, which are usually invoked by fisheries biologists to explain the persistence of discrete local populations in the same waters.

Spatial Isolation

Natal homing has been defined as the return to the natal site for reproduction (Leggett 1977). Clear evidence exists that several anadromous salmonids home to natal areas (Ricker 1972; Harden Jones 1968), including Pacific salmon (Hasler 1966), Atlantic salmon (Saunders 1981, Thorpe and Mitchell 1981), rainbow trout (Biette et al. 1981) and cutthroat trout (Jahn 1969). A certain degree of straying from the natal site was observed in these studies, and the propensity to stray varies both within and between species (Northcote 1978; Kennedy 1981). A variety of orientation mechanisms for both open-water navigation and home recognition have been discussed by Leggett (1977) and Horrall (1981). Bams (1976) has recently demonstrated a genetic component to the natal homing of pink salmon, and Ricker (1972) summarized several studies which suggested that straying increased when fish were transplanted.

Natal homing should be distinguished from the tendency for adults to return to the same spawning sites in successive years, as the latter process has a greater potential for gene flow between local populations and thus results in a different population structure. Such repeated return of spawning adults has been documented for numerous freshwater fish species, including lake trout (Eschmeyer 1955; Loftus 1958; Martin 1960; MacLean et al. 1981), white bass (Horrall 1981), walleye (Colby and Nepszy 1981), and smallmouth bass (MacLeod and MacLean unpublished data). Olson et al. (1978) found that the propensity to return to the same spawning site increases with the number of spawnings, and they suggested that this behavior was due to learning by adults.

It is difficult, if not impossible, to estimate the degree of wandering between local populations. At best, the current

estimates represent minimum levels because of several experimental biases, including incomplete census of spawning grounds, differences in movement patterns of males and females, and the tendency to lump adjacent spawning grounds in defining the home site (MacLean et al. 1981). For reasons discussed in the previous section, however, these estimates of between-site movements will overestimate reproductive straying resulting in gene flow. For example, MacLean et al. (1981) report considerable movement of Lake Opeongo lake trout between spawning shoals, but this may be an elaborate proving behavior (Ricker 1972), and no evidence for gene flow between sites presently exists. Similarly, a small proportion of adult walleyes move between spawning shoals, but the apparent lack of population subdivisions may result from dispersal of larvae or juveniles prior to first spawning (Olson et al. 1978; Colby and Nepszy 1981).

The basis for differences between individuals in the tendency to wander is unknown. A mobile or stray component of populations has been observed in Pacific salmon (Aspinwall 1974), smallmouth and largemouth bass (Lewis and Flickinger 1967; Fajen 1962), longear sunfish (*Lepomis megalotis*) (Berra and Gunning 1970), and several minnows (Kennedy 1981) as well as lake trout (Eschmeyer 1955; Loftus 1958), walleye (Olson et al. 1978; Colby and Nepszy 1981), and lake whitefish (*Coregonus clupeaformis*) (Ihssen et al. 1981a). The proportion of individuals that stray probably depends on many factors, such as the defined size of the home area, as some individuals appear to have larger home areas (Rodeheffer 1941; Lewis and Flickinger 1967), and the age structure of the population, as the tendency to stray may be size- or age-dependent (Larimore 1952; Funk 1957; Kudrna 1965; Olson et al. 1978). An interesting hypothesis for future testing would be that this difference between individuals has a genetic basis.

Temporal Isolation

Differences in the time of spawning can also lead to the reduction of gene flow between local populations. Ricker (1972) suggests that timing of reproduction may, in part, represent a genetic adaptation to local environments. Case histories discussed at this symposium have provided examples of temporal isolation that range from days to years, and have suggested that spawning time is controlled by a combination of genetic and environmental factors that cannot be separated on the basis of present evidence. A few examples are presented to illustrate these conclusions.

Lake trout populations show a wide variety of spawning times that range from June, in Lake Superior, to January, in Lake Tahoe (Martin and Olver 1980). Local populations in the same lake may breed at different times, and commercial fishermen in the Great Lakes discriminated between lake trout types on the basis of spawning time (Goodier 1981; Brown et al. 1981). Discrete groups spawned on the same shoals at different times, with successive peaks separated by 2 weeks or more (Goodier 1981). Spawning generally begins earlier in the north than in the south, both within and between lakes (Martin and Olver 1980; Goodier 1981). River spawning trout in Lake Superior spawned earlier than those along adjacent shorelines (Goodier 1981).

Martin and Olver (1980) review the evidence for effects of abiotic variables such as wind, temperature, and light as modulators of lake trout spawning time, with inconclusive results. MacLean et al. (1981) report that Clearwater Lake lake trout spawned 3–4 weeks earlier, at the same time as the native stock, in Lake Simcoe. Goodier (1981) felt that water temperature has a major influence on spawning times in Lake Superior, but also argued for a genetic component on the basis of successive use of the same shoal by distinctly different groups. Brown et al. (1981) note consistent differences of one or more weeks between Green Lake and Lake Superior strains of lake trout in a hatchery. Berst et al. (1980) demonstrated inheritance of spawning time in female splake.

Biette et al. (1981) described the fall and spring migrations of rainbow trout into streams that flow into the Great Lakes. These migrations are influenced by environmental factors such as water temperature and stream discharge, but Ricker (1972) suggests that the time of migration and spawning of rainbow trout are genetically controlled. Biette et al. (1981) suggest that the development of discrete runs reflects the diverse genetic background of rainbow trout introduced into the Great Lakes.

Timing of spawning is also thought to reduce gene flow between local populations of Atlantic salmon (Power 1981; Thorpe and Mitchell 1981; Saunders 1981). Migrations into the rivers are influenced by river flows, with migrations beginning earlier in the south, but the evidence suggests that the timing of migration represents adaptation to local environments (Schaffer and Elson 1975; Power 1981). Saunders (1981) discusses the early–late run phenomenon, which has both genetic and environmental bases. The repeated stocking of the Penobscot River has resulted in a change of 1 or 2 months in the timing of the spawning migration.

An extreme example of temporal isolation is the odd- and even-year runs of pink salmon (Aspinwall 1974; Allendorf and Utter 1979; Altukhov and Salmenkova 1981). Pink salmon mature at 2 yr of age, with the result that two genetically isolated groups exist, with a small degree of overlap due to other ages (Wagner and Stauffer 1980). Genetic differences between odd- and even-year groups have been clearly demonstrated (Ricker 1972; Aspinwall 1974; Altukhov and Salmenkova 1981), but no agreement has been reached on the reasons for these differences, with explanations based on genetic drift and selection. The recent development of even-year runs in the Great Lakes has been attributed to the spawning of slow-growing 3-yr-olds of odd-year origin (Kwain and Chappel 1978; Wagner and Stauffer 1980), but a genetic mechanism that involves late maturity of slow-growing individuals could be a potential link between the discrete generations.

In summary, a variety of spatial and temporal mechanisms reduce gene flow between discrete local populations. The relative importance of other isolating mechanisms due to behavioral or genetic differences has not been extensively examined. MacLean et al. (1981) have suggested the hypothesis of phenotypic assortative mating to explain the apparent cohesion of planted lake trout stocks in Lake Simcoe. Hay and McPhail (1975) demonstrate the importance of small behavioral differences in reduction of mating between two stickleback morphs. Coadapted gene complexes may prevent the establishment of genes or gene complexes from other local populations. The evidence suggests that both environmental

and genetic modulators are involved in the spatial and temporal restrictions to gene flow.

Life History Strategy and Population Structure

A species life history, or bionomic strategy evolves as a result of environmental pressures acting on phenotype and represents a dynamic set of adaptive traits. In this section, we argue that degree of population subdivision, amount of interaction between adjacent populations, and extent of local adaptation are directly determined by a species bionomic strategy and, in particular, by behavioral traits. We suggest further that apparent species characteristics, such as sensitivity to exploitation, resilience, and re-colonizing ability, are emergent properties of population structure (Altukhov 1981). Hence, a life history strategy provides important clues concerning the way in which the stock concept might best be interpreted and applied for any given species.

The stock concept, as applied to fish populations, is in large measure based on studies of salmonids (Simon and Larkin 1972) and, in particular, on Pacific salmon (e.g. Ricker 1972). Readily observable spatial and temporal separation of spawning aggregations and a high profile socioeconomic role (Larkin 1974, 1981) set Pacific salmon apart as a reference point for evaluation of stock characteristics and population processes in other species. Certain life history commonalities characterize all Pacific salmon — anadromy, natal homing, and a single reproductive effort per life cycle being the most notable. Nonetheless, in spite of the relative uniformity within the genus *Oncorhynchus*, variation in detailed bionomic strategy (size, longevity, fecundity, age of maturity, range, and migration pattern) between species has influenced the way in which exploitation has differentially impacted upon them (Ricker 1981).

Variation in bionomic strategy between Pacific salmon species is much less than among the important groups of Great Lakes species, which range from large, long-lived, late-maturing, low-fecundity forms that have deterministic life history strategies (e.g. lake trout), to small, short-lived, early-maturing species with high fecundities and probabilistic life history strategies (e.g. rainbow smelt). Coregonines, percids, and centrarchids would appear to be intermediate on such an $r-K$ type continuum (Southwood 1976). A need exists to examine the implications of these diverse life history strategies to provide the focus and application of stock considerations in Great Lakes fisheries management. Important life history characteristics can be identified in both adult and juvenile life phases of several Great Lakes species, which might directly influence the amount of interchange between adjacent populations and, hence, influence their discreteness.

Deterministic Versus Probabilistic Behavior

Variation in adult spawning behavior, such as redd digging in sockeye salmon (McCart 1969) versus broadcast spawning in walleye (Colby et al. 1979) would be expected to result in varying degrees of displacement of eggs from spawning areas. Eggs of sockeye and many other salmonines (Bams 1969) are buried within the gravel substrate, and observations of spawning Arctic char (*Salvelinus alpinus*) indicate that loose, unburied eggs are readily eaten by conspecifics (Johnson 1980). Indeed, rainbow trout, cutthroat trout, and Dolly Varden *S. malma*, which are often found with spawning aggregations of *Oncorhynchus*, are important predators of loose eggs. Both nest building and egg predation confine zygotes to the immediate spawning area. In contrast, eggs of broadcast spawners (e.g. coregonids, some percids, osmerids, and clupeids) may be transported considerable distances by water currents. The two modes of spawning behavior suggest varying emphasis on site-specific features, and reflect deterministic versus probabilistic spawning strategies that characterize K- versus r-type species, respectively.

Juvenile behavior of salmonines also contrasts sharply with that of many other species, especially those having pelagic larvae such as coregonines, percids, and clupeids. Walleye larvae are known to be transported considerable distances from hatching sites by wind-generated, subsurface, and surface currents (Houde and Forney 1970). Hence, larval distribution patterns will vary over years, and the possibility arises that progeny from separate spawning sites could come together at localities far from their original spawning grounds within a few days of hatching. Similar circumstances obtain for coregonines (Reckahn 1970) and other species with parallel early life histories. In salmonines, early life history is much more deterministic, in that newly hatched larvae (alevins) remain within the gravel substrate for 1−2 months until the yolk sac has been consumed and the fry are relatively well developed (Dill and Northcote 1970; Mason 1976; Martin and Olver 1980). It is unlikely that progeny from separate salmonine spawning areas would become mixed or that they would be displaced from natal sites during the initial month or two following hatching.

Homing behavior (Ricker 1972) has already been noted as a primary mechanism for maintenance of discreteness between stocks and, in those species known to have strong natal homing tendencies (anadromous salmonines), juvenile and spawning behavior appears to complement the tendency to maintain spatial identity and, hence, to limit genetic exchange with neighboring populations.

Some Great Lakes Examples

Lake trout, a Great Lakes species of major importance, appears to be relatively deterministic in nature, if somewhat less so than the strictly anadromous salmonines. For example, lake trout juveniles remain hidden within the spawning shoal interstices for several months following hatching (Martin and Olver 1980). Horrall (1981) suggests that this behavior may enable juveniles to become imprinted to the natal site and, thus, facilitate homing of adults as in anadromous salmonines. MacLean et al. (1981) describe a complex pattern of prespawning movements of lake trout in which differences occurred between males and females, and younger and older fish. This behavior may indicate extensive proving of the home site (Ricker 1972), although its significance is not yet established. The tendency of lake trout to develop discrete local populations is well illustrated in the Great Lakes (Brown et al. 1981; Goodier 1981), although evidence is based only on phenotypic variation. The relatively unsuccessful efforts to re-establish lost populations (Loftus 1976) or to transplant lake trout, especially when nonnative stocks have been used (MacLean et al. 1981; Plosila 1977) provides further indirect

evidence of genetic differentiation within this species.

In the Great Lakes, numerous geographically discrete spawning areas have been reported for lake whitefish (Casselman et al. 1981; Coberly and Horrall 1980). However, this species appears to be less well differentiated into genetically discrete sympatric stocks (Casselman et al. 1981; Imhof et al. 1980) than might be expected on the basis of allopatric comparisons (Ihssen et al. 1981a; Franzin and Clayton 1977). In view of the generally sedentary nature of lake whitefish (Casselman et al. 1981), and considering the patchy distribution of their habitat, isolation by distance would appear to explain adequately their stock structure in the Great Lakes.

Movement patterns of whitefish in Lakes Ontario and Simcoe indicate a home-spawning range phenomenon (Ihssen et al. 1981a), but considerable movement occurs between spawning shoals, and wanderings may be extensive during other seasons (Budd 1957). Indirect evidence suggests that home-range behavior in this species may be a learned phenomenon. For example, in South Bay of Lake Huron, marginal spawning sites were abandoned in favor of one primary site at low population density (Ihssen et al. 1981a), indicating flexibility in site selection. Indeed, the probabilistic early life history of lake whitefish indicates that little opportunity exists for imprinting (Horrall 1981) to natal sites. The bionomic flexibility of lake whitefish and other coregonines is further suggested by their remarkable phenotypic plasticity (E. G. Lindsey 1981).

Walleye, a species that also exhibits some tendency to home, but perhaps only through an adult-learning process (Olson et al. 1978), and which has probabilistic spawning and juvenile strategies, appears to show little tendency to form discrete stocks (Colby and Nepszy 1981). Another percid, the yellow perch, *Perca flavescens*, has similarly been found to show few genetic differences between sites in Lake Michigan (Leary and Booke 1981). Generally, the differences which have been found among percid populations (e.g. Jarvis et al. 1978) appear to be largely environmentally determined (Colby and Nepszy 1981).

In summary, it would appear that *K*-type life history strategists, having deterministic bionomic adaptations, may exhibit a greater propensity to develop and maintain subdivided populations. It would further appear that species with this strategy could be the most vulnerable to exploitation. This is supported by the difficulty encountered in reestablishment of these species once stocks are lost (e.g. Larkin 1981; Saunders 1981; Helle 1981; Ricker 1972) and, in contrast, by the persistence and/or resilience of *r*-type species having probabilistic bionomic strategies (e.g. whitefish and walleye in the Great Lakes). Other species in the Great Lakes such as lake herring have been less persistent, in spite of similar probabilistic life histories. Invasion of the Great Lakes by small planktivores (rainbow smelt and alewives) may have had greater impact on lake herring (Smith 1972; Anderson and Smith 1971), independently of other stresses.

Implications for Management

In previous sections, we have argued that the gene pools of fish species are hierarchically subdivided by a variety of barriers to gene flow. A variety of morphological, ecological, and biochemical tools is available to distinguish between these discrete groups (Ihssen et al. 1981b), and evidence has been presented that indicates the importance of the ecological and genetic differences between these groups for maximization of long-term production. We have also argued that the structure of subdivided populations is the result of behavioral processes that are one component of a set of coadapted traits, which collectively constitute a life history strategy.

A logical conclusion for the above argument might be that each discrete group of fish should be identified as a stock and managed separately, with the goal of harvesting so as to preserve all genetic variation, and planting fish so as to restore all lost variation. However, this ideal goal is usually not attainable for a variety of social and economic reasons. We argue that a stock concept needs to be adopted by managers in order to introduce a genetic perspective, which must be integrated with ecological viewpoints before realistic decisions about appropriate compromises between biological and socioeconomic costs can be reached. In this section, we discuss a few examples to illustrate the need for this revised conception of fish populations.

If population subdivision is an adaptive result of a set of coadapted life history traits, then stresses which tend to modify that structure will alter the pattern of genetic variation and, consequently, cause a decline in overall fitness. For example, homing of walleye appears to be a learned adult behavior, so that the precision of homing will depend on the age structure of the walleye population. Exploitation of large, older individuals will tend to increase straying and gene flow between local populations and, thus, reduce the total genetic variation of the population. Differences in the pattern of prespawning movement between sexes and ages of lake trout will cause differences in their vulnerability to stationary fishing gear (MacLean et al. 1981). Impact of exploitation on the social organization and gene flow between local populations of lake trout is uncertain, but may be of considerable importance. Natural selection may result in genetic differences between year-classes, hence harvesting that is selective by age could reduce the total genetic variation in the population through restrictions on inter-year-class breeding. The ecological implications of selective exploitation on iteroparous species has been discussed by Murphy (1967, 1968), who suggested that a loss of older Pacific sardine year-classes led to a collapse in the fishery after two consecutive unsuccessful spawnings.

Local adaptation in subdivided fish population is argued for by the failure of transplants of Pacific salmon (Ricker 1972; Bams 1976; Altukhov 1981) and the difficulties in restoring lost runs of anadromous species (Larkin 1981; Saunders 1981). Thorpe et al. (1981) argue that the sensitivity of fish populations to stress appears to be related to the degree of population subdivision and, thus, the extent of local adaptation. The challenge for managers will be to develop tactics to preserve this genetic variation in order to maintain and restore fisheries resources.

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THORPE, J. E., AND J. F. KOONCE (WITH D. BORGESON, B. HENDERSON, A. LAMSA, P. S. MAITLAND, M. A. ROSS, R. C. SIMON, AND C. WALTERS). 1981. Assessing and managing man's impact on fish genetic resources. Can. J. Fish. Aquat. Sci. 38: 1899–1907.

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Assessing and Managing Man's Impact on Fish Genetic Resources[1]

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Historically, human activities have adversely affected the genetic resources of many fish species. We suggest that a continuum of vulnerability to loss of genetic resources exists for fishes. Primary determinants of vulnerability are extent of stock structure in populations and fundamental life history features, such as length of juvenile period, sex ratio, and fecundity. The genetic basis for this trend is the relationship between the subdivided state of a population (its stock structure) and important processes of genetic change, which include selection, gene flow, and genetic drift. We relate various human activities to their effects on genetic resources through these genetic processes, and we review various lines of evidence for a relationship between stock structure and genetic diversity. In general, we found that those species whose populations are subdivided into nearly isolated stocks (e.g. Pacific and Atlantic salmon) are more vulnerable to directional changes in genetic composition as well as reduction in overall genetic diversity through loss of some stocks. We also found that similar changes will be difficult to detect, if they occur at all, in less stock-structured species like walleye.

Key words: stock structure, genetic diversity

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Les activités humaines ont historiquement exercé une influence défavorable sur les ressources génétiques de plusieurs espèces de poissons. Nous avançons l'hypothèse qu'il existe chez les poissons un continuum de vulnérabilité à la perte de ressources génétiques. Les principaux facteurs qui déterminent cette vulnérabilité sont la structure par stock au sein des populations et les caractéristiques fondamentales du cycle biologique, telles que durée de la phase juvénile, proportion des sexes et fécondité. Les fondements génétiques de cette tendance sont la relation entre les subdivisions d'une population (sa structure par stock) et d'importants processus de changement génétique, dont la sélection, le flux génique et la dérive génétique. Nous établissons la relation entre diverses activité humaines et leurs effets sur les ressources génétiques par le truchement de ces processus génétiques et passons en revue les preuves d'une relation entre structure par stock et diversité génétique. Nous constatons qu'en général les espèces dont les populations sont divisées en stocks presque isolés (p. ex. les saumons du Pacifique et le saumon atlantique) sont plus vulnérables que les autres à des changements dirigés de composition génétique de même qu'à une diminution, par perte de certains stocks, de diversité génétique globale. On a aussi découvert qu'il sera difficile de détecter de semblables changements chez des espèces moins structurées par stock, telles que le doré jaune.

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REDUCTION in the genetic resources of natural fish populations has become an important fisheries management problem. Much of the reduction is due to various human activities. Not only has the genetic diversity of many fish populations been altered, but many thousands of populations and species have been extirpated by pollution, overexploitation, habitat destruction, and other human developments. Concern with reduction of genetic resources in fish is part of a larger global concern for the genetic resources of the biosphere (cf. Harlan 1981), and a number of possible approaches have been advocated (e.g. Loftus 1976; FAO 1981, Maitland et al. 1981). These approaches address two slightly different aspects of genetic resources: conservation of gene pools and conservation of genetic diversity. In this paper, we focus exclusively on the issue of genetic diversity. Our purpose is to relate the stock concept to the mechanisms by which various human activities alter the genetic diversity of fish populations.

That fish species are subdivided into stocks is a widely accepted notion. The genetic basis of these stocks, however, is not well understood. For common reference, we use a stock definition proposed by Ihssen et al. (1981): A stock is an intraspecific group of randomly mating individuals with spatial or temporal integrity. The advantage of this stock concept is that it links genetic diversity of a fish population and various human activities through well-known mechanisms of population genetics.

Genetic diversity of population is determined in part by its genetical structure (Wright 1951). The aspects of population structure that are important in this context are age composition, sex ratios, and extent of population subdivision. Truly random mating probably does not occur in any natural fish population. Instead we see a wide range of population subdivision from nearly isolated subunits as in some of the anadromous salmonids to nearly panmictic populations. The extent of population subdivision and the migration rates among the population subunits are, therefore, important attributes of the species. In fact, the stability of the genetic diversity of a population has been associated with the persistence of the subdivided state of the population (Altukhov 1981), and Giesel (1974) showed theoretically that polymorphism, which can be related to population subdivision, increases population stability. As has been often argued (Wright 1977), therefore, population subdivision is an adaptive property of the species. In our usage, a stock is equivalent to a subdivision unit of a population. On the issue of genetic diversity, however, our focus remains with the population as a collection of stocks (i.e. its stock structure).

Understanding the influence of alteration of population stock structure on genetic diversity requires consideration of the processes regulating gene frequencies. As Wright (1951) discussed, these processes can be classified as directional (i.e. bring out directed changes in gene frequency) or nondirectional (indeterminant in direction, but determinant in variance of gene frequencies). For our purposes, selection and immigration (or gene flow) are the main directional processes, and drift (sampling error and founder effects) is the nondirectional process. That these processes affect genetic diversity of a population is well established in genetic theory (Wright 1951; Falconer 1960), and their interaction with the state of population subdivision determines the genetic diversity of the population.

Human activities affect these genetic processes in various ways. Selection, in general, is a process by which a genotype's future contribution to the next generation is limited, and it is the dominant mode of human interaction with fish populations. Size-selective fishing gear, habitat, elimination, alteration of forage community, pollution stress, and other such activities can impose new selection pressures on a stock or may alter the existing selection forces. In any case, there will be a change in the relative fitness of various genotypes,

and gene frequencies will change until a new steady state is obtained. Artificial selection is a direct human determination of the relative fitness of the genotypes in the stock, and it has been employed to: (1) increase body weight (Donaldson 1970; Kincaid et al. 1977; Moav et al. 1978), (2) change average spawning date (Donaldson 1970), and (3) increase abundance of rare genetic variants for use as genetic tags (Utter et al. 1976). Because artificial selection may rely on small effective population sizes, artificial selection may result in more rapid decrease in genetic diversity because of the simultaneous effects of drift.

Gene flow among stocks is the primary determinant of the discreteness of individual stocks. Migration among stocks is thus a characteristic attribute of the population. With greater migration (or straying rate) between two stocks, similarity of stocks also increases, and, in this way, migration can counteract the effects of selection and drift. However, migration rates among stocks are not necessarily constant. Fluctuations in environmental conditions and population density may cause considerable variability in migration rates. Obviously, therefore, human activities that affect movement of fish either directly through erection or removal of barriers or indirectly through changes in population density or environmental conditioning have the potential to alter genetic diversity of the population. Human activities related to these changes are habitat alteration, transplantation of exotic stocks, introduction of hatchery-reared strains, and overexploitation.

The final process linking human activities to genetic diversity is drift. Genetic drift is the dispersal of allele frequencies through time and space. Loss of genetic diversity in finite populations through drift is usually associated with the notion of sampling variability (Falconer 1960). Two aspects of the loss of genetic variability are important to this paper. First, in each generation there may be a loss of heterozygotes due to random inbreeding, and second, in each generation there is a chance that an allele may be lost from the population. In both of these cases, the changes in genetic diversity between generations is inversely proportional to two times the effective population size, where the effective population size is determined by the relative contribution of each sex to the next generation (Falconer 1960). Considering these two features of drift in a subdivided population, an individual stock is likely to show a loss of genetic diversity through both a reduction in heterozygotes and a loss of some alleles each generation. Each stock in the stock complex, however, will behave differently. Consequently, the stock complex will have greater genetic variability than an equivalent sized panmictic population (Falconer 1960). Human activities should, therefore, accelerate the genetic drift process significantly whenever stock densities are lowered to a range of effective population size of 100 or less, depending on allele frequency.

Our summary of these genetic processes and their influence on genetic diversity is a direct outgrowth of a concern for rehabilitation of some fisheries and protection of others (e.g. Loftus 1976). From a rehabilitation view, it is important to know whether a stock represents a unique biological adaptation. Altukhov (1981) implies that focus on single stocks may be inappropriate and that the stock complex is a better representation of the adaptedness of a species. Regardless of which view of adaptation is better, the existence of such a wide range of stock complex seems to indicate that the response of a species to stress from human activities will depend to a large degree on its genetic and phenotypic variability. Fisher (1930) has argued that rates of evolution are directly proportional to genetic variance, and Wright (1977) has added that the most conducive circumstances for rapid evolution are the process of population subdivision (stock formation in our usage) and variable environmental conditions for each of the population subunits. If one of the goals of management is the preservation of the adaptive potential of a species, then conservation of genetic diversity and preservation of stock structure will become linked goals. Assuming a direct relationship between adaptability and genetic diversity, we might expect some species to be more adaptable to human-induced stress than others. For our purposes, however, the central question is to what extent is maintenance of stock structure important to preserving the adaptive potential of various species. Because of the complex relationship among the various genetic forces and population subdivision, it is difficult to make an a priori case for the importance of stock structure. Therefore, we now summarize some findings about the susceptibility of various species to loss of genetic variability due to human activities.

Summary of Effects of Human Intervention on the Genetic Structure of Populations

We begin this summary with human intervention mediated through selection. The primary activity is fishing, and a well-documented example comes from the oceanic fisheries for salmon (*Oncorhynchus* and *Salmo* spp.). Exploitation in this case occurs before individuals segregate into discrete stocks, which disperse to reproduce in specific river systems (Altukhov 1981; Helle 1981; McDonald 1981; Power 1981; Ricker 1981; Saunders 1981; Thorpe and Mitchell 1981). These stocks seem to be very vulnerable because they cannot be fished in strict relation to their numerical strengths and biological characteristics. Furthermore, the concentration of the terminal fishery on reproductive animals increases the potential for selection. In fact, these fish show some dramatic examples of apparently heritable phenotypic changes in response to various fishing practices.

Ricker's (1981) summary of average changes in size and age of Pacific salmon indicated that life history and the size-selective nature of the fishery determine the overall selection pressure produced by a fishery. Pink salmon (*Oncorhynchus gorbuscha*), which mature uniformly in their 2nd year of life, have decreased in size by 10−40% over a 25-yr period. It is important to note that these changes reflect alteration of growth rate only and are not complicated by alteration of age composition of catch. Ricker (1981) was thus able to calculate a heritability coefficient (in the broad sense) of 0.22 to 0.3 for various fishery regions. Size and age composition of the catch also seem to have changed in chum salmon (*O. keta*) as a response to selection against rapid growth. According to Ricker, sockeye salmon (*O. nerka*) has shown an equivocal pattern of changes, as has coho salmon (*O. kisutch*). The absence of consistent patterns in these two species may reflect ambivalent effects of selection and/or buffering by hatchery-liberated fish. In contrast, the average size and age of chinook salmon (*O. tshawytscha*) has decreased by 50% and 1 year, respectively, since 1925−30, and this trend appears everywhere from California to Alaska.

Although Atlantic salmon (*Salmo salar*) are iteroparous, size and age changes seem to be consequences of fishing activities as well (Parrish and Horsted 1980). Martin and Mitchell (1981), for example, argue that selective removal of older fish by the West Greenland fishery has reduced the percentages of 2- and 3-sea-winter fish in Scottish commercial catches. Because of a general inverse relationship between river age and sea age among many individual river stocks (Thorpe and Mitchell 1981), these trends could result from selection against fast growth and late maturity. In addition, the dominance of females in the 2-sea-winter age-groups implies an alteration of sex ratio by the fishery. Given evidence that many of these characteristics have genetic components (Saunders 1981), therefore, fishing activities certainly have the potential to induce directional genetic changes and possibly to reduce genetic diversity in Atlantic salmon.

More than fishing, however, other human activities associated with habitat alteration (construction of dams, deforestation, pollution, etc) have caused considerable loss of Atlantic salmon stocks (Saunders 1981). Attempts to restore some of these stocks indicate that important genetic adaptations were lost with the stocks. Saunders argued that appropriate timing of both spawning runs and smolt runs were required for successful restoration. That these have been difficult to attain emphasizes the losses of unique genetic resources in this species.

The Atlantic and Pacific salmons represent one extreme of population subdivision. As Altukhov (1981) stated in his review, these species can show extremely complex stock structure. For the unfished Lake Azabach sockeye salmon, for example, the population consists of 30–40 distinct spawning groups, which were distinguishable through LDH-B_1 and PGM gene frequency differences (Altukhov 1981). As discussed above, much of the fishing exploitation occurs during periods of stock mixture, and any directional changes in gene frequencies occur and are observable in this mixed stock state. The influence of fishing and habitat alteration on overall genetic diversity of the species is thus difficult to interpret. In general, however, and depending upon the degree of local adaptation and effective stock size, the loss of stocks can be interpreted as a loss of overall genetic variance. Also, the fact that some small river stocks may be more drastically reduced than are others (Piggins 1980) indicates that mixed stock fisheries may accelerate drift effects on local stock genetic diversity. Because of the central importance of these nearly isolated stocks to the genetic diversity of the species, vulnerability of individual stocks of these and related species (Ricker 1972) suggests that recognition of their stock structure will be required for rehabilitation and conservation management (cf. McDonald 1981; Saunders 1981).

Extension of these findings about the salmonids to other species whose populations have less stock structure is difficult. Local adaptation was a key to making inferences about the effects of selection on genetic diversity, and decreased stock structure means less potential local adaptation. The percids, for example, often show some group differences in the Great Lakes, but there is little-known genetic basis for these differences. Colby and Nepszy (1981) imply that much of the apparent stock differences in walleye (*Stizostedion vitreum vitreum*) may be environmental in origin, although there is some question about the genetic basis for behavioral preference for spawning area. Yellow perch (*Perca flavescens*) seem to be similar.

Yellow perch in Lake Erie, for example, can be classified into three major groups by growth rate: western, central, and eastern basin stocks (Petzold and Paine 1978). However, differences in growth rate may be primarily environmental (Kitchell et al. 1977; Colby and Nepszy 1981). Other more minor stocks appear to be isolated from these major stocks (e.g. Scott 1955; Teleki 1975; Petzold and Paine 1978). The extent of mixing of the major stocks is not well known. Thorpe (1977) reports little migration of perch in large water bodies, but Rawson (1980) found highly variable migration rates among groups of perch tagged in various portions of the western and central basins of Lake Erie. With the observation of little genetic difference between groups of yellow perch (*Perca flavescens*) in Lake Michigan (Leary and Booke 1981), it appears that differences in yellow perch stocks within each of the Great Lakes may have a very strong environmental component.

Although its genetic basis is unclear, growth rates of yellow perch have declined over the past 50–60 years. Like pink and chinook salmon, these declines in growth rate are associated with levels of exploitation. For the period 1927–37, Jobes (1952) reported that a minimum length for 100% mature female yellow perch was 236 mm. By 1976, this minimum length became more variable by basin and showed an overall decrease western basin, 190 mm; central basin, 196 mm; and eastern basin, 226 mm (Petzold and Paine 1978). Again, however, as in the question of genetic stock structure, there is no evidence that these changes are heritable. In fact, as suggested by Ricker (1981), size-selective fisheries may not always select against fast growth and early maturity. During some portions of the life history and in some special circumstances, the relative fitness of rapid growth may be greater than for slow growth.

One aspect of selection for which there is abundant information in agriculture is the development of resistant strains of pest species (Harlan 1981). This potential, but unintended, consequence of selection is applicable to the sea lamprey control program and deserves some comment.

To protect valuable sport and commercial fishes from predation by sea lamprey (*Petromyzon marinus*) in the Great Lakes, selective lampricides (TFM and Bayer 73) have been applied to infested streams to kill the ammocoetes. Lampricide treatments have been conducted since 1958, with the frequency of treatment on individual streams varying from 1 to 13 applications from 1958 to 1978 (Smith and Tibbles 1980; Pearce et al. 1980). Because lampricide treatments are not completely effective, resistance to stream treatments may be favored. For example, it is possible that four or five generations of sea lamprey have been exposed to TFM and survived to reproduce. If sea lamprey develop a resistance to lampricides, the negative effect on rehabilitation of Great Lakes fish stocks will be enormous as there are no existing substitute control methods that are as effective. Further, in many streams ammocoetes move into lentic areas off the stream mouths, where they may be exposed to treatment by bottom toxicants, but escape rates can be high either through impossibility of total area coverage, or through sublethal dosages. Thus, changed habitat preferences may increase fitness. In addition, spawning populations of adult sea lamprey appear to

be increasing in connecting waters of the Great Lakes, such as the St. Mary's River between Lakes Superior and Huron. Survival of progeny from these spawnings will favor spawning in this and similar cold waters, for which current lamprey eradication measures are inadequate (Lamsa et al. 1980).

Among newly established year-classes following lampricide treatment, competition has been reduced, growth rates have increased, and transformation to the adult form is possible sooner (Purvis 1979). If lampricide treatments are delayed, earlier maturity may be favored. Among adult lamprey populations, reduction in abundance has increased the average size and shifted the sex ratio from an abundance of males to an abundance of females (Heinrich et al. 1980). As a result effective population fecundity is greater than abundance information alone would indicate.

Directional changes in allele frequencies may also be caused by gene flow. Because the stock structure of a population is determined in part by the rates of migration of individuals, any alteration of migration patterns will result in changes in the genetic diversity of the population. As in the case of selection, a stock structure consisting of many nearly isolated stocks would seem more vulnerable than less-structured populations. Again Altukhov's (1981) summary of genetic studies of Pacific salmon in the USSR provides some examples. These studies show two basic results of transplantation experiments (representing a major change in gene flow patterns). Either the transplants were a complete failure or significant reduction in overall population fitness occurred. The transfer of fertilized chum salmon eggs from the Kalininka to the Naiba River is a good example of the latter response (Altukhov 1981).

Between 1964 and 1971, 350 million fertilized chum salmon eggs were transferred from the Kalininka to the Naiba river, USSR (Altukhov 1981). By 1969–70, MDH-C frequencies of the Naiba stock had shifted towards those characteristic of the donor stock. But the Kalininka chum showed return rates in the Naiba river of only 10–20% of those expected in their original river. From 1964 on, the composite return rate of all chum in the Naiba river fell from a previous mean value of over 0.5% for the Naiba stock, to a new mean of less than 0.2%. The population size fell from 650 000 spawners in 1968 to a recent mean level of 30–40 000, which illustrates an adverse consequence of massive genetic migration of nonadapted genotypes.

The reasons for introduction failures and the reduced fitness of the populations where successful seem to be the same. Local stocks represent adapted groups of individuals. The apparent failures of Atlantic salmon rehabilitation in New England Rivers, for example, may be due to genetically based behavioral traits for timing of spawning and smolt runs (Saunders 1981). Stocking of hatchery-reared fish may be a particular problem in this regard (cf. Hynes et al. 1981), and introgression of wild stocks is a potentially troublesome consequence of introducing inappropriate hatchery strains (Helle 1981; Kreuger et al. 1981).

Whether these reductions in fitness due to influx of new migrants are permanent is unclear, but the evidence suggests they may be persistent. Historical changes in the *Coregonus* populations resulting from introductions to Lago Maggiore illustrate this point well. Between 1860 and 1880, *C. wartmanni coeruleus* and *C. Schinzi helveticus* were introduced from Bodensee (Berg and Grimaldi 1965; Grimaldi 1972). Their natural hybridization resulted in a single species (the Lavarello) that maintained a stable population until the 1950s. At this time *C. macrophthalmus* (the Bondella) was introduced from Lac de Neuchatel. The Bondella increased rapidly until it dominated among the *Coregonus*. However, its gill-raker number increased from 34 to 37.7, which seems to be a directional change in genotype (Berg 1970; see Lindsey 1981). The cause of these changes is not clear, but it should be noted that artificial propagation of the Lavarello form was practiced for over 50 years with an average of 20 million fry added per year. The Bondella, in contrast, has not been the object of artificial propagation. Evidence for long-term consequences of stocking has also been obtained by Ryman and Ståhl (1981) in some Swedish lakes. In an area of Sweden known to have been stocked in the past, they reported heterozygote excess at AGP-2 locus in brown trout (*Salmo trutta*) populations. This excess is not observed in over 100 undisturbed natural populations of this species, and Ryman and Ståhl argued that stocking led to the breakdown of existing reproductive barriers among stocks of brown trout. The original stock structure thus seemed lost.

Evidence for drift-related changes in fish populations due to human activities is less than for the previous two genetic processes. The main area of effect seems to be in hatchery practices (cf. Hynes et al. 1981). A variety of evidence suggests that hatchery practices may lower genetic diversity (Allendorf and Phelps 1980; Ryman and Ståhl 1981). Furthermore, there seems to be additional evidence that domesticated strains have lowered adaptive capacities in natural settings (Reisenbichler and McIntyre 1977; Fraser 1981; Webster and Flick 1981). It seems that losses of genetic diversity should be balanced carefully against techniques that allow sperm from a single male to fertilize the eggs of 1000 to 10 000 females (Petit et al. 1973; Billard 1977). In addition to drift effects in hatcheries and hatchery strains, however, human activities could accelerate loss of alleles when natural populations fall to low densities. This situation may now exist for some Atlantic salmon stocks (Piggins 1980). More importantly, genetic drift may interfere with our perceptions of stock structure and local adaptation. As Allendorf et al. (1981) show, even with high migration rates, the existence of 20 groups can result in a variety of genetic differences due to drift alone, if only a few loci are examined.

Theoretical Analysis of Selection by Fishing

From the examples summarized above, there is good evidence that a range of human activities affect genetic diversity and frequency of genotypes in fish populations. The effects of selective fishing, however, are problematical. In some cases, such as Pacific pink salmon, historical size changes can be attributed to the reduced fitness of fast-growing genotypes by a size-selective fishery. In other cases in which age composition and size change, the interpretation becomes more complicated. Because most Great Lakes species are iteroparous and have overlapping generations among the spawning adults, the risks of size-selective fishing to stock structure, genetic diversity, and genetically based changes in fishery productivity are difficult to determine. To help sort out what

Ricker (1981) called ambivalent selection in such cases, we include the following brief theoretical analysis.

Population subdivisions in most Great Lakes species are observable only during spawning and a variable period of embryonic, larval, and juvenile development. Mixture of stocks is a general feature of many species, and it is this mixed stock state with which management is most concerned. In the best data situations, information on growth and population dynamics would allow application of a variety of theoretical tools, which exist to assist the development of management strategies (e.g. Garrod and Jones 1974; Walters 1975; Shuter et al. 1979; Kutkuhn 1981). Basing management on aggregate characteristics of a subdivided population, however, may lead to undesirable reductions in the genetic resources of the population. At least two different views on the management of subdivided populations were expressed at STOCS. Altukhov (1981) viewed a stock complex as an adapted entity and argued that management must be spread over component stocks equally if the overall stock structure and its adaptedness are to be preserved. Others, such as Power (1981), offered convincing evidence that some stocks, by virtue of their special situations, are much more vulnerable to overexploitation. In these situations, there seems to be a need to manage each stock independently of the larger stock complex.

Although we cannot fully evaluate such views here, we can explore the consequences of overexploitation on hypothetical stocks of some typical Great Lakes species. Because of the ready availability of stock–recruitment data and population models for Western Lake Erie walleye (Shuter et al. 1979), we will use this species to explore the effects of exploitation on the persistence of two hypothetical stocks and to determine the expected selection pressures on growth rate produced by current fishing practices in Lake Erie.

For convenience, we will assume that these two stocks are reef spawners and river spawners. Further, we assume that the reef stock is numerically dominant and that random environmental factors affect both stocks equally. We also assume that the river stock has a longer average juvenile period than the reef stock (all the reef individuals of age III and older are mature and all river-spawning individuals of age IV and older are mature). Using a procedure similar to that of Garrod and Jones (1974), we can calculate that the river population would then have a long-term optimal effort of 0.3 per year, while the reef stock's optimal effort would be 0.52 per year. Long-term simulations of these stocks at various constant effort levels suggest that overexploitation of the combined fishery affects the river stock more dramatically than the reef stock (Fig. 1a–d).

Despite their hypothetical origin, these results suggest some general consideration for evaluating risk of exploitation to subpopulation structure in species like walleye. The critical information required for this risk assessment is a characterization of the life history of each of the identifiable subpopulations. To the extent that subpopulation structure is observable during spawning, length and fertility at age may be estimated for various subpopulations (e.g. Casselman et al. 1981). With these data and information on the vulnerability of different-sized individuals to the fishing gear, it is then possible to establish two risk categories. In the case of little or no heritable difference in the catchability and fertility schedules of the subpopulations, then it is unlikely that exploitation will

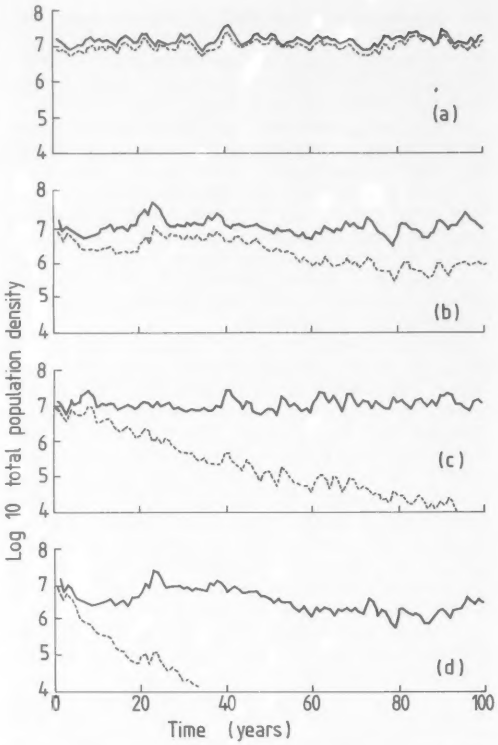

FIG. 1. Effects of various constant effort fishing strategies on two mixed stocks of walleye in western Lake Erie (reef stock, solid line, and river stock, dotted line). Effort levels in the sumulations are (a) 0.4, (b) 0.6, (c) 0.8, and (d) 1.0 per year.

lead to a reduction in subpopulation structure. Even overexploitation will only reduce the rarer subpopulations by an amount proportional to their initial density relative to the dominant stock density. However, one might also expect that some lower absolute size limit exists at which a subpopulation may be likely to suffer some catastrophic decline (e.g. Beddington and May 1977; Peterman et al. 1979). In the second case of substantial difference in fertility or catchability, one may reasonably expect that even slight overexploitation can lead to alteration in subpopulation structure.

Given patterns of exploitation of walleye in Western Lake Erie from 1947 to 1969, overexploitation seems to have been a dominant management problem (Regier and Hartman 1973; Nepszy 1977; Shuter et al. 1979). Although we have no direct observations of walleye subpopulation structure during this period, we might expect a reduction of population substructure to accompany this history of overexploitation. Based on the trends summarized in Fig. 1, we suggest that subpopulations with earlier maturity and/or decreased catchability should have increased relative to other subpopulations. The mixed fishery, therefore, would tend to reflect the attributes of this "selected" stock.

There are, of course, many ways that the life history characteristics of these two hypothetical stocks could be determined. If these differences are produced by heritable growth rate differences, then the assumption of the model that catchability of various ages is the same for both stocks may not be realistic. Again using an approach analogous to that of Garrod and Jones (1974), we can look at the effects of different growth rates on catchability, age of first reproduction, and optimal effort for maximum sustainable yield. To accomplish this, we simply assume that both mean age of first recruitment to the fishery and mean age of first reproduction of females are proportional to growth rate. The results for three genotypes representing fast, average, and slow growth are summarized below:

	T_M	Q	F_{opt}
Fast growth	3.6	1.77	0.35
Average growth	3.8	1.97	0.34
Slow growth	4.0	2.2	0.34

where T_M is the average age of first reproduction, Q is the average age of first recruitment to fishery, and F_{opt} is the optimum instantaneous fishing mortality (per year). Because the optimal exploitation characteristics are essentially the same, there seems to be little basis to speculate that the fishery will increase the fitness of the slow-growing genotype. If anything, these results imply that rapid growth and thus early maturity might be attributes having greater fitness under the current fishery selection regime; an observation that Ricker (1981) also made. With these results, however, we do not want to imply that fishing is unlikely to be a source of selection pressure in species like walleye. It is conceivable that some genotypes could exist that typify the results in Fig. 1. For example, Ihssen (personal communication) has suggested that some genotypes might exist that divert reproductive energy into growth. Such a genotype would, in our examples, result in early entry to the fishery, but delayed maturity — a most vulnerable condition (see Fig. 1).

Conclusions

The theoretical example of the response of walleye stock structure to exploitation and the historical examples discussed above indicate that vulnerability to human activities varies with specific life history features of species. Increasing awareness that a species' bioenergetics and life history characteristics can be used in a priori evaluation of management strategies (e.g. Ware 1980) has led to a fundamental recognition that groups of species along an $r-K$ continuum may have to be exploited differently. Although, as indicated by Colby and Nepszy (1981), the $r-K$ characteristics of a species may change with geographic location, recognition that some species are more vulnerable to overexploitation than are others is an important guide in helping managers decide on priorities of assessment and management options. Adding concern with genetic resources to these productivity considerations, therefore, would also seem to require statement of the relative vulnerability of various species to genetic alteration by human activities.

From our examples, a measure of the stock structure of the population is an important attribute for this purpose. If one assumes that life history characteristics and the subdivision state of populations have been determined by natural selection, then a population's stock structure is an adaptive characteristic of a species (Wright 1977). The overall population stability and perhaps even its persistence may thus depend on maintenance of stock structure. Although one cannot exclude historical artifact, the examples we have summarized seem to indicate that species with nearly isolated stocks are most susceptible to loss of genetic diversity. Losses of runs (stocks) of salmon are readily apparent as is the difficulty in restoring them, and genetic theory clearly indicates that loss of these stocks decreases the overall genetic variability of the population. One way of approaching this characterization would be the partitioning of genetic variability within and between stocks as suggested by Krueger et al. (1981).

Stock structure would thus form one axis of a vulnerability response surface for fishes. Polymorphism and specific life history attributes, such as length of juvenile period, sex ratios, and fecundity, certainly could be included as other axes. The effects of fishing as a selective force in populations, for example, seems to vary with specific fishery practices and life history characteristics of the species. Convincing evidence for selection against rapid growth is available for pink salmon, but such a selection seems less likely for walleye in Lake Erie. We cannot be sure of any generalizations from these findings, but we do recommend future research on the existence of hierarchies of stress vulnerability as fruitful and necessary.

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Perspectives and Policy Recommendations on the Relevance of the Stock Concept to Fishery Management[1,2]

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The Stock Concept International Symposium (STOCS) addressed a broad range of concerns about the relationship between intraspecific stocks and their genetic and environmental origins. STOCS produced an understanding of the stock concept that makes it possible to develop operational stock definitions reflecting the key elements of concern to fishery managers. These definitions can change as circumstances dictate because stocks represent states in a dynamic process. Extensive life history information available for Great Lakes fish provides a basis for estimating the significance of intraspecific stock structure in management of these species. Recognition of the potential for stock formation is important for evaluating the impact of management actions and for planning the restoration of individual species in fishery rehabilitation programs. Finally, we present a brief set of recommendations for research and management based on our perception of the stock concept and its relevance to fish community rehabilitation.

Key words: fish stocks, fishery rehabilitation

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Au cours du STOCS (Stock Concept International Symposium), on a abordé un large éventail de problèmes touchant la relation entre des stocks intraspécifiques et leurs origines génétiques et environnementales. Ce colloque a permis de mieux comprendre le concept de stock et d'en arriver à des définitions opérationnelles qui reflètent les préoccupations majeures des gestionnaires des pêches. Les stocks étant une phase d'un processus dynamique, ces définitions pourront être modifiées selon les circonstances. Grâce au volume considérable de données sur le cycle biologique des poissons des Grands Lacs, nous disposons maintenant d'une base sur laquelle juger de la signification de la structure de stocks intraspécifiques pour la gestion de ces espèces. Il est important de reconnaître le potentiel de formation des stocks quand il s'agit d'évaluer l'impact de diveres mesures de gestion et de planifier le rétablissement d'espèces individuelles dans des programmes de réhabilitation de la pêche. Enfin, nous faisons quelques recommandations touchant la recherche et la gestion, fondées sur notre perception de la notion de stocks et sur sa pertinence quant à la réhabilitation des communautés de poissons.

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STOCS was conceived by K. H. Loftus as a means of examining the applicability to freshwater fisheries of the stock concept which has been the cornerstone of Pacific salmon management. In recent years there have been impressive advances in research related to the stock concept, but with few exceptions (e.g. Loftus 1976; Simon and Larkin 1972), the results of this research are scattered throughout the scientific literature. The technical papers in these proceedings further enhance our understanding of the concept while consolidating some of the recent research on the intraspecific stock structure of fish populations. The synthesis contributions examine the implications of the stock concept for management activities such as fish culture, fisheries regulation, and conservation of genetic fish resources. We hope that the perspectives developed in this concluding paper reflect the strong consensus expressed by symposium participants that an understanding of the biological basis for intraspecific stocks will further enhance our opportunities for preservation, rehabilitation, and management of freshwater fish resources. We suggest an approach which will ensure consideration of the implications of stock structuring for those species of management interest.

Symposium Findings

Conceptualization of processes at different levels of organization is a useful initial step toward understanding responses at higher levels. Biologists find it convenient to index the process of evolution by cataloguing its biological manifestations as species. Designation of species does not preclude the existence of races, tribes, demes, or other entities commonly assumed to reflect additional levels of organization within species. Each of these population units serves to define some functional genetic aspect of the larger species unit in time or space (Ihssen et al. 1981), thus providing indicators of the state of the underlying process of evolution.

Loftus (1981) challenged STOCS participants to develop a stock ... "definition which can be meaningful in management." Collectively these proceedings demonstrate that we have gone a step beyond this challenge by identifying those key elements of the stock concept that make it generally applicable across a broad spectrum of fish communities. It is no longer necessary to question whether freshwater fish of management concern (including cultured species) are comprised of discrete stocks; henceforth this will be a management assumption. This result provides an opportunity to develop operational definitions that may be applied to specific management problems.

One approach to developing an operational definition might be to paraphrase an earlier definition so that it reflects the key elements of concern to a manager. For example, Bailey and Smith (1981) define stocks ... "as local populations that maintain recognizable genetic differentiation by separation of their spawning place or time." A manager concerned about the preservation of a particular morphological variant of a species might replace the word "genetic" in this definition with "morphological," thus providing for the existence of stocks exhibiting environmentally induced characteristics, while preserving key elements of the stock concept, i.e. temporal and spatial discreteness and reproductive segregation. An operational definition should allow change as circumstances dictate because it seeks to represent a state in a dynamic process. We conclude that it is not necessary to agree on a single definition of a "stock" to communicate the implications of the concept for fisheries management.

Perhaps the single most important result of STOCS is the emergence of a strategy for protection or rehabilitation of fish communities. One problem faced by resource managers is the uncertainty of knowing which genes or gene combinations should be preserved in specific management or enhancement situations. The strategy to address this problem is simply to apply genetic principles in manipulating wild and domestic fish populations so as to minimize the genetic impoverishment of individual species. In operational terms this often means preserving the greatest possible degree of genetic variability in the populations in question. It follows that individual stocks must be preserved (or maintained) if a significant amount of the total genetic variability in the population occurs between rather than within stocks. This strategy presupposes but does not depend on the existence of discrete intraspecific stocks. It also maximizes management options by retaining the opportunity for future manipulations of genetic resources. The small genetic variation within a species might be centered in discrete stocks within a basin, or more broadly in allopatric stocks across the range of the species. The key to management strategy is to identify those species most likely to consist of populations whose existence depends on the occurrence of discrete intraspecific stocks. This will allow managers to assign priorities in accordance with each species' sensitivity to destructuring following the loss of discrete stocks. By "destructuring" we mean a reduced ability to maintain reasonable levels of productivity in the fish community. Similarly, managers can evaluate current fishery management measures and rank them according to their relative impact on individual stocks.

Since it is unrealistic to expect empirical knowledge of stock structure for even a small part of the species we intend to manage, we must infer from the life history of each, the relative vulnerability of that species to destructuring by the loss of discrete stocks. (Conversely, we may examine the prospects for the species' rehabilitation by a stock reconstruction process.) Our present understanding of the major constituents of the Great Lakes fish community (for example) is sufficient to indicate the possibilities for spatial and temporal flow of genetic information between stocks. We offer the following interpretive model as a means of estimating a species' potential to form discrete stocks as a function of some of its life history characteristics. It may be useful to develop further interpretations based on behavioral attributes or reproductive guilds (Balon et al. 1977) or by constraining candidate species to a single functional group, family, or other taxon, e.g. rank Pacific salmon in order of their likelihood of stock formation, or contrast the possibilities for *r*-selected versus *K*-selected species (MacLean and Evans 1981).

It is clear that species producing minute and fragile fry (e.g. *Coregonus clupeaformis* and *C. artedi*) that emerge during tempestuous spring weather (Faber 1970) have little physical capacity for resisting transport along vast stretches of exposed shoreline. Thermal bars, coastal jets, and thermal instability of the littoral zone water mass might reasonably be expected to ensure some mixing of fry from geographically adjacent stocks. Fry transported away from their natal shoals might then settle when their locomotory powers are suffi-

ciently developed that they are no longer at the mercy of the currents. Such a life history might be expected to lead to stocks which are morphologically differentiable, as a function of the various environments where the postlarvae settle (i.e. the environmentally determined stocks of Ricker 1972, p. 145), while being relatively homogeneous genetically. In addition to morphological differences apparent between areas, we might also expect to find some variation in stock features from year to year. Lake Huron whitefish (*Coregonus clupeaformis*) stocks described by Casselman et al. (1981) are representative of this class of life history patterns.

By contrast, there are species such as lake trout (*Salvelinus namaycush*) with fry that are relatively sedentary in the substrate of their natal shoals after hatching. On completion of yolk sac absorption and emergence, these fry are strong swimmers, bottom-oriented, and unlikely to be swept into a foreign environment. These fish should be capable of spatially preserving the genotypes conferred by their parental stock, even without invoking an imprinting and homing hypothesis. Genetic mixing between geographically adjacent stocks at spawning time would occur to an extent determined by the seasonal mobility of the species within its normal habitat in the lake. Species of this type might also exhibit temporal isolating mechanisms based on differing spawning times as described for Lake Superior lake trout (Goodier 1981). These species would tend to form recognizable "genetic stocks," i.e. the hereditarily determined stocks defined by Ricker (1972, p. 145).

Temporal differences in life history patterns could also be important in determining a species' potential for stock formation. Pacific salmon (*Oncorhynchus* spp.) depend on a variety of age-classes of spawners. In contrast, walleye (*Stizostedion vitreum vitreum*) are long-lived and sustained by multiple age-class spawnings. Genotypically, we would expect greater similarity between years in walleye stocks than we would expect for Pacific salmon. Temporal "straying" for these stocks is accomplished on the one hand by extended periods of fertility for multiple-spawning species, and on the other hand by various ages of fish in spawning runs. Pacific salmon provide an opportunity to examine the magnitude of this temporal straying, given genetic markers assignable to individual year-classes (Helle 1981).

Generalizing from these cases, we would expect to see the greatest opportunity for formation of geographically discrete genetic stocks among fishes such as lake trout (*Salvelinus namaycush*) which are long-lived, bottom-oriented during the fry stage and multiple-spawning. Species at the other extreme, (e.g. yellow perch (*Perca flavescens*), which are short-lived, pelagic as fry, and dependent on very few age-classes in the spawning stock) should have the least propensity to form discrete genetic stocks. The extent to which species of either type would form "environmental stocks" is probably related more to their overall morphological plasticity than to specific life history attributes. Drawing from Great Lakes experience (Table 1), we demonstrate one approach to examining the potential for stock formation. This approach assumes that we know enough of the natural history of the species to judge the degree of "locomotor determinacy" conferred by the life history pattern of the fry or postlarval stages.

The greatest opportunity for stock development in freshwater fishes would seem to exist in species such as lake trout, which possess protracted juvenile life stages. Perhaps this is related to the potential for extended periods of imprinting, leading to greater precision in homing. Little opportunity exists for between-years stock isolation in species with repeat or multiple age-class spawners unless little straying occurs between geographically discrete stocks.

The morphological manifestations of environmental stocks tend to be continuous variables, e.g. variations in pigmentation, linear dimensions, or rates such as growth and mortality. Species such as the coregonines, possessing a broad unbroken range in expression of these traits, are most often those for which environmental stocks are distinguishable.

Understanding the opportunities for stock development as a function of the behavioral and life history characteristics of the species enables us to design management measures to minimize impact on the stock development process. This is the rationale underlying recommendations for rainbow trout management in the Great Lakes (Biette et al.1981). More generally, it is important that fishery management activities protect or enhance those biological features of a stock that set it apart from others of the same species. In terms of fishery exploitation, this is the converse of the selective breeding approach which propagates animals from the extremes of the distributions of certain characteristics. The implications of this conclusion for husbandry of stocks with special attributes such as deep swimming ability or resistance to certain diseases are detailed by Hynes et al. (1981).

A final implication of our perception of stocks is that fisheries management should include deliberate provision for maintaining opportunities for gene flow between stocks of wild populations. Sanctuaries have long been utilized to provide a recolonization potential for surrounding geographic regions. The temporal analogue of spatial sanctuaries is seasonal closures, which might be generalized to include cyclical or irregular annual closures for certain species.

Major Information Gaps

A major outcome of the symposium has been recognition of the need for information regarding mechanisms for the development and maintenance of stock structure in fish populations. Speculation abounds on the roles of imprinting and homing for freshwater fishes. Horrall (1981) emphasized the importance of distinguishing between the recurrent appearance of adults on spawning shoals and true homing to natal sites. There seems to be little disagreement on how important homing might be, but little evidence on how important homing actually is for maintaining discrete stocks (MacLean et al. 1981). If homing is critical to the process, then it is clear that imprinting must occur for some Great Lakes species almost instantaneously on hatching, e.g. for smelt, suckers, whitefish, and walleye (Table 1).

Hynes et al. (1981) drew attention to the need to recognize the effects of domestication and inbreeding in fish cultural practice. We are still unable to determine the extent to which inbreeding and small effective population sizes are contributing to apparent differences in gene frequencies in samples from wild stocks (R. C. Simon personal communication), but

TABLE 1. Classification of some Great Lakes fishes according to their potential for stock formation. Question marks indicate substantial uncertainty. Life spans reflect estimates for lightly exploited or unexploited stocks. Determinate fry are those capable of significant locomotion with respect to their habitat. Indeterminate refers to fry that are relatively vulnerable to transport by water currents.

Species	Life history characteristics					Environmental stocks	Potential for genetic stocks		Empirical evidence of stocks
	Life span (yr)	Spawning		Fry ecology/duration					
		Frequency	Mode	Determinate	Indeterminate		Temporal	Spatial	
Lake trout (*Salvelinus namaycush*)	8–20	Multiple	Group	Moderate		Common	Moderate	Moderate	Goodier (1981)
Rainbow trout (*Salmo gairdneri*)	5–10	Multiple	Paired	Extensive		?	?	Strong	Biette et al. (1981) Utter et al. (1973)
Pink salmon (*Oncorhynchus gorbuscha*)	2	Single	Paired	Brief			Strong	Moderate	Helle (1981)
Deep-water coregonines (*Coregonus sp.*)	3–5	?	?		?	Common?	?	Weak?	Todd (1981)
Whitefish (*Coregonus clupeaformis*)	4–15	Multiple	Group		Brief	Evident	Weak	Weak	Casselman et al. (1981)
Walleye (*Stizostedion vitreum vitreum*)	4–15	Multiple	Group		Moderate	Common (blue pike?)	Weak	Weak	Colby and Nepszy (1981)
Yellow perch (*Perca flavescens*)	3–8	Multiple	Group?		Brief	Common	Weak	Weak	Thorpe et al. (1981)
Sea lamprey (*Petromyzon marinus*)	4–16	Single	Paired	Extensive			Weak	Strong	Krueger and Spangler (1981)
Alewife (*Alosa pseudoharengus*)	3?	?	Paired		?	Not evident	?	Weak	?
White sucker (*Catostomus commersoni*)	3–8	Multiple	Group		Brief		Weak	Moderate	Beamish (1970)
Burbot (*Lota lota*)	4–13	Multiple	Group		?		?	Weak	Muth and Smith (1974)
Rainbow smelt (*Osmerus mordax*)	3–8	Multiple	Group		Brief	?		?	?

recent advances in cryogenic gamete preservation (Erdahl and Graham 1980) may alleviate this problem in fish culture.

Most geneticists agree on the need for better estimates of the rate of exchange of genetic information between stocks as a basis for understanding the potential of certain stocks to adapt to new or changed environments. The recent appearance of significant numbers of 3-yr-old pink salmon in Lake Superior (Kwain and Lawrie 1981) provides an unusual opportunity to examine the exchange of information between temporal stocks of this species.

It is clear that some biologists interpret observable differences between groups of fish as though they were strictly genetic in origin, e.g. strains of rainbow trout (Kamloops, McCloud River, Donaldson, Shasta). Many of the characteristics distinguishing these strains could be subjected to critical examination in carefully designed experiments to segregate genetic and environmental components (Utter et al. 1973). The heritability of critical life history characteristics, such as autumn vs. spring spawning in rainbow trout, needs further work. Berst and McCombie (1975) observed that a fall-spawning hatchery stock of rainbow trout reverted to spring spawning under natural conditions within the planted generation.

For the Great Lakes fish community, inspection of Table 1 reveals that we are less knowledgeable about the existence of stock structuring in the smaller species than we are for top-level piscivores. Perhaps this is because management efforts are typically directed at the larger members of the food chain, but the possibility exists that stock structuring is less important (and less conspicuous) for species with relatively short generation times. Ryder et al. (1981) emphasized the need to examine ecosystem responses to perturbations in terms of generation time, rather than absolute (arbitrary) time scales. This is fundamental to understanding stock differences recently made apparent by studies utilizing electrophoretic methods (Ihssen et al. 1981).

The ecosystem consequences of changes in intraspecific stock structuring are not yet known, but the existence of discrete stocks would seem to represent an additional degree of complexity in the fish community. If Caswell (1976) is correct in the assertion that complexity increases a community's ability to absorb perturbations in the face of environmental variation, then we might infer that a sequential loss of discrete stocks would predispose a species (and perhaps an entire fish community) to eventual catastrophic collapse. This could explain the community collapse in the Upper Great Lakes pursuant to the fishing-up process described by Regier and Loftus (1972). Hill and Durham (1978) suggest that functionally similar species, which they label "homotactic congeners," exist in similar (homotaxial) positions within a community, lending a kind of redundant control on the biological system. This prompts us to question whether stocks might serve a comparable function in fish communities. It is possible that the deepwater coregonine complex conferred a vital stability on the salmonid community of the Great Lakes during the first half of this century.

Applications and Recommendations

Many recommendations concerning the technical and theoretical components of stock analysis and management policies appear in detail in the technical and synthesis papers of these proceedings. In the following recommendations we attempt to identify broad classes of the most urgent concerns relating the stock concept to fishery rehabilitation and management.

Research

Stock discreteness — Although substantial progress has been made in understanding stock structures in fish populations, the gaps identified earlier in our information base suggest that some critical unknowns must be addressed. In spite of recent improvements in our ability to detect differences between stocks, mere detection of those differences provides little or no insight into the questions of how they arose, whether they are genetically based, or whether they relate to stock fitness or to fitness of the stock complex as a species within a particular aquatic system.

An appropriate place to pursue this research would be to re-examine some of the fundamental assumptions concerning present fish populations. For example, we are impressed with the extent to which morphological variants of a species can coexist within a lake basin, with little evidence of genetic differences between stocks (Casselman et al. 1981; Todd 1981). It is conceivable that the deep-water coregonines (*Coregonus* sp.) and blue pike (*Stizostedion vitreum glaucum*) of the Great Lakes have never been "good" species, but existed as environmentally induced morphotypes, developing their peculiar characteristics in response to differences in hydrostatic pressure, diet, or other environmental factors. Developmental polymorphisms in other organisms have been shown to have been caused by such simple mechanisms as intake of single dietary nutrients (Gilbert 1980). We suspect that a thorough review of the coregonine literature, including especially the transplantation results of Steinmann (1951) and Svärdson (1965), would provide valuable insights into the possible significance of environmental and genetic stocks in the maintenance of salmonid communities.

Additional research is necessary to relate behavioral ecology to mechanisms of stock maintenance. Horrall (1981) argued vigorously for the importance of imprinting and homing in the maintenance of discrete stocks. Altukhov, (1981) on the other hand, illustrated the importance of information flow between generations in a sockeye salmon (*Oncorhynchus nerka*) stock. Explicit estimates of gene flow between temporally or geographically discrete stocks remain to be developed.

Heritability and fitness — It is crucial to understand the extent to which stock differences are associated with fitness. Since fitness is the relative ability of an organism to survive and transmit its genes to the next generation (King 1974), it is important to know the heritability of fitness traits such as growth, life expectancy, and reproductive characteristics. The relatively sudden prominence of pink salmon in Lake Superior, following seven or eight generations of low abundance, raises the possibility that specific adaptations in fitness traits have occurred in this species since its introduction to Lake Superior in 1956.

RECOMMENDATION: *That research be intensified to resolve further the existence of genetic and environmental stocks and mechanisms underlying their maintenance or persistence in wild populations. This research should include intensive studies of gene flow within and between stocks to determine the risks associated with the extirpation of discrete stocks.*

MANAGEMENT

We recognize that long-term improvements in fishery resources can most likely be achieved by directing fisheries policies toward the overall ecosystem, rather than being narrowly constrained to a lower level of organization, as in a single-species approach. Two areas of management activity that should be examined in light of the stock concept include fish cultural practices and fishery regulation.

Fish cultural practices — Fish culture facilities have frequently emulated practices common to other areas of animal husbandry. While these measures may be appropriate for the production of maximum numbers or poundages of fish, STOCS participants recognized the need for reexamination of the role of hatcheries in fisheries management directed toward rehabilitation of self-reproducing stocks. An appreciation of the stock concept dictates that this role involve the maintenance of genetic diversity within the brood stocks and the hatchery product. Krueger et al. (1981) propose two strategies to maximize genetic variability in the hatchery product. Both strategies require knowledge of the range of genetic variability available within the cultured species. Insidious or inadvertent selection in the hatchery, coupled with substantially greater risks of inbreeding and overt selection for characteristics that may have little to do with survival in the wild, have been identified as common consequences of traditional practices (Hynes et al. 1981).

RECOMMENDATION: *That fishery agencies concerned with the rehabilitation of self-reproducing stocks re-examine fish culture practices in light of the stock concept according to the specific concerns raised by Hynes et al. (1981), and that hatchery stocks designated for release in wild environments be carefully evaluated with respect to their potential genetic impact on extant populations.*

Fishery regulation — Fishery exploitation invariably seeks to utilize a significant part of wild fish resources. The key to sustained yield management of these resources has traditionally been the determination of how large the extraction could be without acting to the long-term detriment of the resource. For many years we have recognized the shortcomings of a simple quantitative evaluation of fishery impact (Larkin 1977). It is now clear that more complex quantification is necessary, and that qualitative factors relating to the life history of the fish may be extremely important with respect to the genetic character of the stocks. Maintenance of genetic diversity in fish resources is now seen as essential to stability of fish communities (Ryder et al.1981) and to the long-term productivity of individual species (Thorpe et al. 1981). It is particularly hazardous to engage in fishery practices that selectively exploit differences within fish stocks based on fundamental characteristics of the life history of that species exploiting a stock either early or late in a spawning period (Thorpe et al. 1981).

The implications of this conclusion in formulating fishery policy are that we must seek to avoid regulations which mold the exploited stocks into a life history pattern that departs significantly from their original (evolutionary) character, e.g. changing the age structure (especially variance) of the spawning population, and differentially exploiting spawning runs through inappropriate timing of seasonal closures. In the latter case, if seasonal closures are set in such a manner that they effectively exploit only the limits of the distribution of spawning times, substantial change can be inflicted on the onset and duration of spawning runs (Vaughan 1947). In the former case, it now seems unreasonable to exploit multiple-spawning species, such as whitefish and lake trout, to the extent that their age structures emulate the life history pattern of fishes evolved to reproduce only once during their lifetime, i.e. Pacific salmon. Thus, the Abrosov (1969) approach for multi-age spawning stocks may be extended to include consideration of the variance of the distribution of spawning age-classes as well as the mean.

RECOMMENDATION: *That fishery regulatory mechanisms be developed so as to protect exploited species from selective exploitation of stocks exhibiting the extremes of vital life history characteristics, such as sexual dimorphisms, early or late spawning, size, and growth.*

Conclusion

This symposium has been extremely stimulating and timely. We hope that these Proceedings have established a bench mark on the present state of the science. The synthesis papers have built on the divergent points of view expressed by STOCS participants to promote a broader understanding of the stock concept, especially as it relates to freshwater fishes. The differences of viewpoint and opinion that remain should provide fertile ground for research.

In view of the rate at which this branch of science is advancing, it might be useful in a few years to convene a similar conference, to review the positions held at the time of STOCS and what will have been achieved in the interim.

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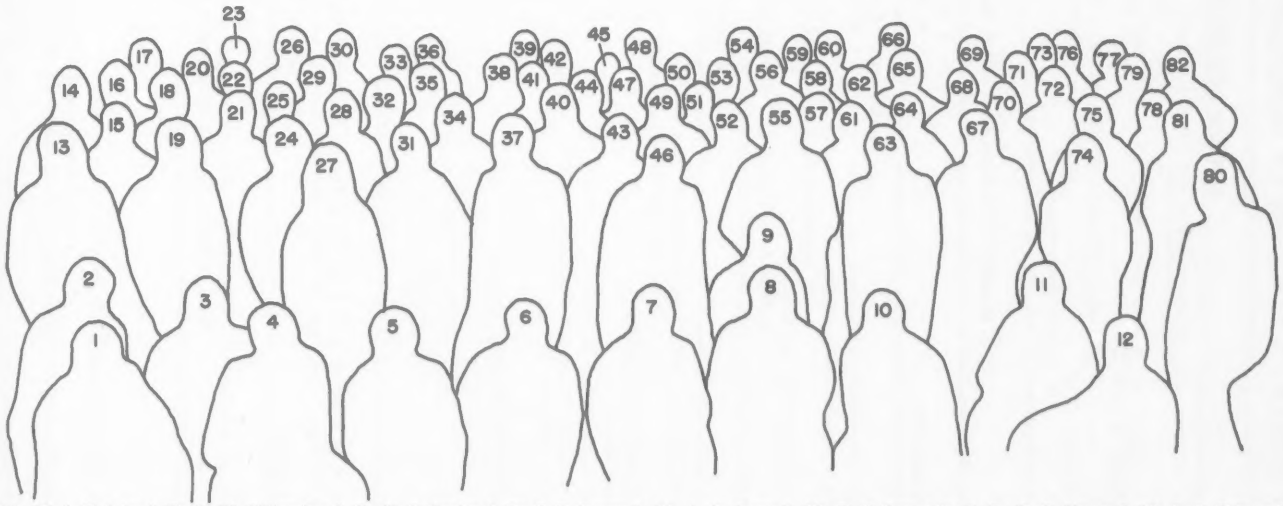

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